SWARD CANOPY STRUCTURE AND INGESTIVE BEHAVIOUR IN GRAZING ANIMALS

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I hereby declare that this thesis has been composed by myself, and except where otherwise stated, the work contained herein is my own.

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ABSTRACT

Evidence from the literature regarding the sward characteristics which determine ingestive behaviour and herbage intake in the grazing ruminant is contradictory and inconclusive. Variation in sward height has usually been confounded with concomitant changes in sward density, and often digestibility, making objective interpretation difficult.

In the current work, a series of grass and cereal swards was produced using different seed rates at sowing in an attempt to obtain a large and independent variation in sward height and density. These swards were grazed within three months of sowing to minimise differences in maturity and digestibility. A few established ryegrass swards were also grazed, and in the second of the two experiments grazing or cutting pre-treatments were employed to increase further the range of sward conditions.

Experiment 1, run over two grazing seasons, comprised a series of trials on 33 large plots which were stocked with sheep and cattle (1983) or just sheep (1984). Swards were grazed down over eight days whilst changes in sward canopy structure, ingestive behaviour and herbage intake were measured.

The quantity of cattle data collected was limited, but results for the sheep clearly indicated that bite weight had the dominant influence on herbage intake. Bite rate and grazing time tended to increase as bite weight and intake declined, both during the defoliation of a sward and when comparing responses between swards. Bite weight was strongly influenced by bite depth, and the sheep generally grazed deeper, taking heavier bites, when the sward was taller and more digestible. The bulk density of the grazed sward stratum had a minor, and unexpectedly negative, effect on bite weight. Possible explanations are given.

A substantial proportion of the variance in both bite depth and bite weight was attributed to undescribed differences between crops. Since indoor feeding trials did not indicate any intrinsic herbage qualities which significantly influenced voluntary intake, these differences probably reflected unmeasured structural variables.

Experiment 2, run in 1984, involved a more controlled approach than the large plot trials. Sheep were confined in cages and allowed to take only 20 bites from small patches of sward. Measurements of bite weight, depth, area and volume were related to the characteristics of seventeen contrasting swards.

Surface height had a strong positive effect on bite depth, and consequently bite volume and bite weight both increased on taller swards. The variables which determined bite area were less obvious, but within a given grass species bite area appeared to be related positively to surface height and negatively to the population density of grazed plant units.

Grazed stratum bulk density, which varied independently from surface height, also had a positive effect on bite weight. The relative importance of these two key sward variables in determining bite weight varied with the range of sward heights under consideration. Their effects, however, were independent and additive, producing a planar joint response surface.

The advantages of the new grazing cage technique are discussed and suggestions made for further studies.

CONTENTS

FIGURES

TABLES

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GLOSSARY

The following abbreviated or common names of crops, and abbreviations of plot or sward names, technical terms, chemical symbols and formulae and statistical conventions, are used in this thesis.

Crops

		Scientific name
Agrostis		Agrostis tenuis
am. PRG	dwarf cultivar of perennial ryegrass normally sown on amenity areas.	Lolium perenne
barley		Hordeum vulgare
oats		Avena sativa
PRG	perennial ryegrass	Lolium perenne
PRG1	perennial ryegrass established for one year	Lolium perenne
PRG4	perennial ryegrass established for four years	Lolium perenne
red fescue		Festuca rubra
rye		Secale cereale
timothy		Phleum pratense

Plots or swards

L, M, H	plots sown at low, medium or high seed rates respectively (Abbreviations also apply to the resultant swards)
T, B	top and bottom (location of the PRG1 plots in the field)
Lg, S	long and short (descriptors of the PRG4 swards)
P	swards pre-cut using hand-held clippers
G, C	regrowths following grazing (G) or cutting with a reciprocating mower (C)

Technical terms and chemical symbols and formulae

Cr	chromium
Cr_2O_3	chromic oxide
DM	dry matter
DOM	digestible organic matter
IVOMD	*in vitro* organic matter digestibility
K_2O	potash
LW	live weight
N	nitrogen
NDF	neutral detergent fibre
OM	organic matter
OMD	apparent digestibility of organic matter
P_2O_5	phosphate

Statistical conventions

CV	coefficient of variation
d.f.	degrees of freedom
F	variance ratio
r^2	proportion of variance accounted for by a regression, calculated from $\left(\frac{\text{regression sum of squares}}{\text{total sum of squares}}\right)$

s.d.	standard deviation
s.e.	standard error (of a mean)
s.e.d.	standard error of a difference between means
n.s.	not significant at the 0.05 level of probability
*	significant at the 0.05 level of probability ($P<0.05$)
**	significant at the 0.01 level of probability ($P<0.01$)
***	significant at the 0.001 level of probability ($P<0.001$)

"...in this case, the grass being quite fresh, and of a sufficient length for a full bite, it would please their palate so much, as to induce them to eat it greedily, and fill their bellies before they thought of roaming about..."

Anderson (1797)
discussing the grazing
management of beef cattle

INTRODUCTION

Grasslands cover at least one-third of the land surface of the globe (Breymeyer and Van Dyne, 1980). Grazing lands provide essentially all the nutrients for numerous species of large wild herbivores, and the majority of the nutrients for domestic livestock, and the cheapest forms of animal production are based on grazing (Van Dyne, Brockington, Szocs, Duek and Ribic, 1980; Morley, 1981).

The importance of the level of herbage intake in determining - and indeed often limiting - the productivity of the grazing ruminant has been recognised by many workers (Stobbs, 1973a; Stobbs and Hutton, 1974; Minson, 1980; Zemmelink, 1980; Allison, 1985; Leaver, 1985). Hodgson (1982a) stated that whereas the digestiblity and metabolisablity of the grazing ruminant's diet may each vary by a factor of about two, the animal's intake may vary by a factor of at least four, even when grazing conditions are relatively unrestricted.

It is important, therefore, to understand the factors influencing the herbage intake of grazing animals as this is a prerequisite to identifying the scope which exists for manipulating intake (Hodgson, 1982a; 1985a). Current knowledge of the animal/sward interface is limited (Lazenby, 1981; Anderson, Smith and Hulet, 1985; Hodgson 1986). Although many studies have been conducted to investigate the influence of sward canopy structure on the ingestive behaviour and herbage intake of grazing sheep and cattle, many of the results appear to conflict. Moreover, in most studies the effects of some or all of the basic sward variables - herbage mass, height, density and digestibility - have been confounded, obscuring the relationships.

There is a need to define more closely the patterns and ranges of sensitivity in the ingestive behaviour and herbage intake responses to changes in sward variables, and to determine the relative importance of the different sward variables in specific circumstances. Such information is required for determining priorities in plant breeding and selection, and for the management of swards and grazing animals (Hodgson, 1985a).

The project which forms the basis of this thesis was devised in an attempt to isolate the independent effects of the important canopy structure variables on ingestive behaviour and herbage intake. The main experiment involved a series of large plot grazing trials run over two grazing seasons, using both sheep and cattle in the first year but only sheep in the second year. This experiment was supplemented in the second year with a more detailed study of the bite dimensions of grazing sheep, an area of research hitherto largely unexplored.

LITERATURE REVIEW

Introduction

In any grazing situation, the herbage intake of the ruminant is influenced by a very wide range of animal, sward and environmental factors. The major factors are indicated in Figure 1, with bold type denoting those factors which were of particular interest in the grazing trials reported in the Experimental section of this thesis. This Literature Review concentrates on these key factors, examining the available data on the effects of canopy structural characteristics on the selectivity and ingestive behaviour of the animal, and its consequent herbage intake. Most of the information cited relates to sheep and cattle, and comparisons are drawn between these two species where possible.

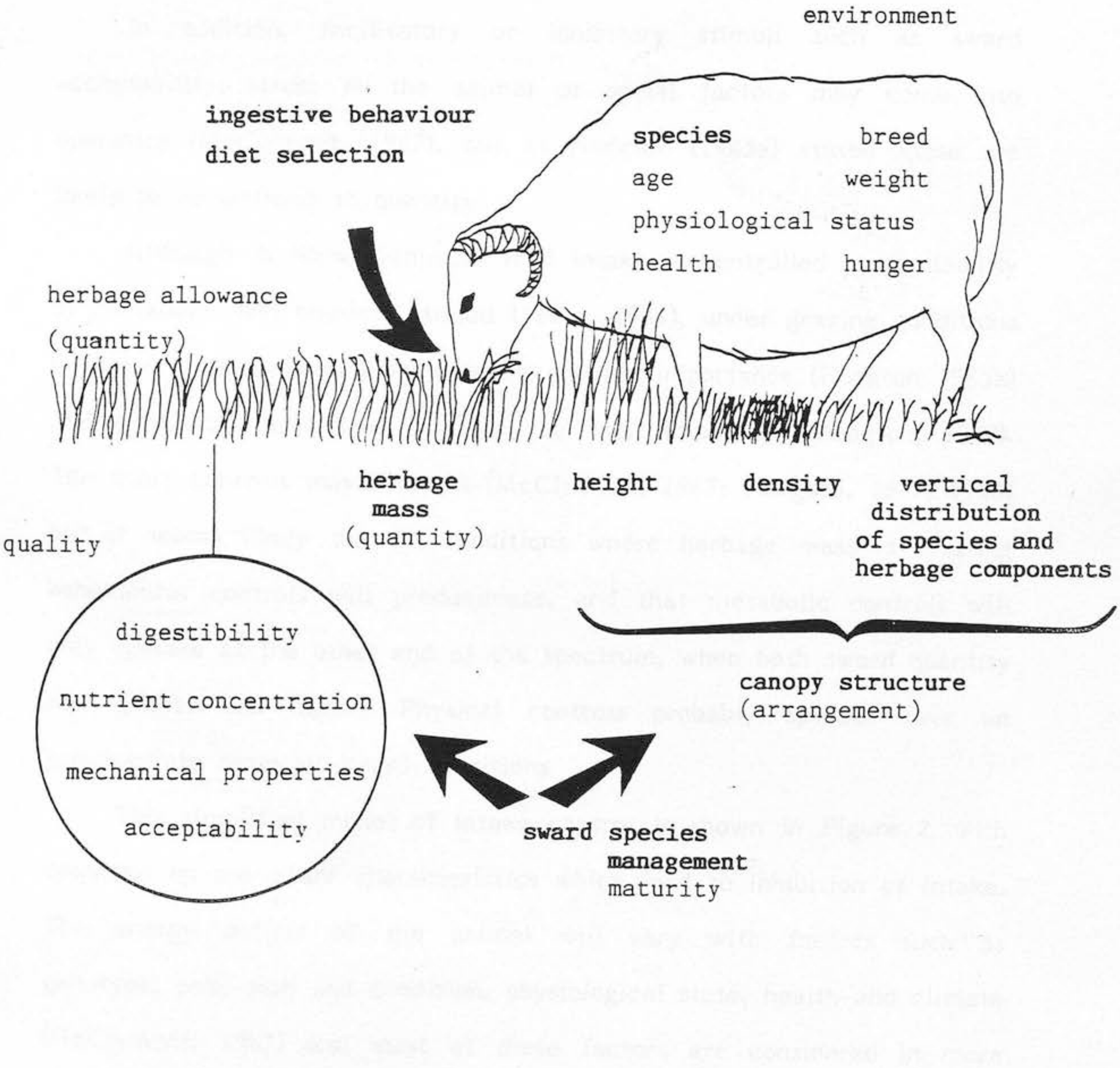
After a brief review of the control of herbage intake and how intake may be influenced by sward quality, quantity and arrangement, the various ingestive behaviour variables, including bite dimensions, are discussed in turn in relation to herbage mass and canopy structure. The interrelationships between herbage intake, the behaviour variables and sward variables are considered next, and the influence of management, the environment and animal characteristics mentioned briefly. Finally, diet selection is discussed and in particular its interaction with sward conditions, ingestive behaviour and intake.

The control of herbage intake

The control of herbage intake in the grazing animal has been reviewed by McClymont (1967), Arnold (1970), Hodgson (1977, 1985a, 1986), Freer (1981) and Allison (1985). Following McClymont (1967), Moore (1983) and Hodgson (1985a), the control of intake in grazing animals may be envisaged as a balance between a facilitatory feeding drive (due to the nutrient or energy deficit of the animal) and three

Figure 1

Factors influencing herbage intake in grazing animals



sets of inhibitory stimuli. These are:

a. metabolic, arising from the concentation of metabolites in the bloodstream;

b. physical, reflecting the volume of digesta and retention time in the rumen;

c. behavioural, reflecting the animal's ability firstly to maintain its short-term rate of intake when sward conditions are limiting, and secondly to increase its grazing time if rate of intake does decline.

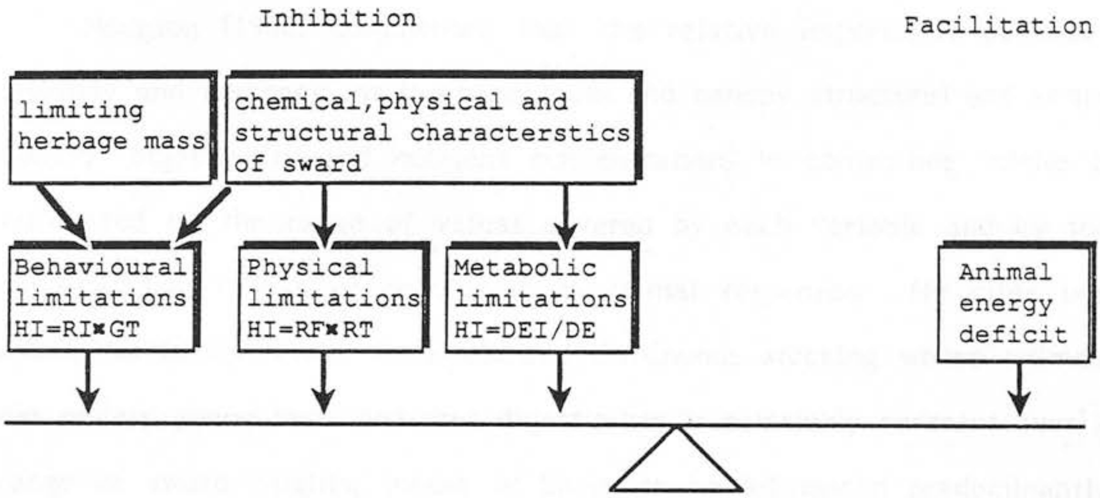
In addition, facilitatory or inhibitory stimuli such as sward acceptability, stress to the animal or social factors may come into operation (McClymont, 1967), but as Hodgson (1985a) stated these are likely to be difficult to quantify.

Although in housed animals food intake is controlled predominantly by metabolic and physical stimuli (Freer, 1981), under grazing conditions behavioural limitations assume much greater importance (Hodgson 1985a) and metabolic limitations may be the least important (Hodgson, 1986). The three controls may interact (McClymont, 1967; Hodgson, 1977, 1986) but it seems likely that in conditions where herbage mass is limiting behavioural controls will predominate, and that metabolic controls will only operate at the other end of the spectrum, when both sward quantity and quality are high. Physical controls probably operate over an intermediate range of sward conditions.

This simplified model of intake control is shown in Figure 2, with emphasis on the sward characteristics which lead to inhibition of intake. The energy deficit of the animal will vary with factors such as genotype, body size and condition, physiological state, health and climate (McClymont, 1967) and most of these factors are considered in more detail at a later stage in the Review.

Figure 2

A conceptual model showing the balance between inhibitory and facilitatory stimuli which control herbage intake in the grazing ruminant Sward characteristics which influence the behavioural, physical and metabolic limitations are also indicated. (After McClymont, 1967; Moore, 1983; Hodgson, 1985a)



DE digestible energy content of herbage
DEI digestible energy intake
GT grazing time
HI herbage intake
RF rumen fill
RI rate of intake
RT retention time

Under optimal foraging theory, grazing animals should select sward components which yield the highest net rates of energy intake (Illius, 1986). Thus, when an animal is grazing in a selective manner it may opt for a diet with a higher energy content if this more than compensates for any reduction in rate of intake. Selective grazing adds another dimension to the relationships between ingestive behaviour responses and sward canopy structure and is considered further in a later section of the Review.

Hodgson (1986) commented that the relative importance of sward quantity and arrangement (herbage mass and canopy structure) and sward quality (digestibility and nutrient concentration) in controlling intake is influenced by the range of values covered by each variable and by the corresponding ranges of sensitivity in animal responses. He cites two examples: firstly, under well-balanced continuous stocking where animals eat mainly young leaf, and diet digestibility is relatively constant over a range of sward heights, intake is likely to be influenced predominantly by behavioural limitations caused by canopy structure.

Secondly, under rotational grazing where both nutritive value and canopy structure change progressively as the sward is grazed down, making it more difficult to assess the relative importance of each of these factors, behavioural limitations are still likely to be important. Herbage intake under rotational grazing has been shown to be closely related to herbage allowance (the weight of herbage per animal or per kg LW per day) even when diet digestibility remains constant. For example, when Greenhalgh, Reid, Aitken and Florence (1966) reduced the herbage allowance of cows from 24.9 to 11.3 kg DM cow^{-1}d^{-1}, mean daily intake fell from 12.6 to 10.8 kg OM cow^{-1} but mean diet OMD fell only from 0.756 to 0.750. This suggested that herbage mass and perhaps canopy structure, rather than sward quality, had the dominant effect on intake.

Whilst this Review concentrates on the influence of sward quantity and arrangement on herbage intake, some aspects of the influence of sward quality are considered briefly here. Since protein levels in grass are normally adequate for the grazing animal, at least in temperate conditions (Baker, 1976) where the grass species are relatively free of specific toxins (Jones, 1981), the level of fibre in the diet and its physical composition tend to have the greatest influence on intake (Minson, 1982). Various experiments have found a positive linear relationship between voluntary intake and herbage digestibility (Freer, 1981). Minson (1982) stated that intake is controlled by the proportion of indigestible residue in the feed, transit time of the residue through the rumen, and the size of the rumen. Feeds vary in the length of time taken for breakdown to particles small enough to leave the rumen, and intake/digestibility relationships may vary for: leaf compared with stem; different pasture species and cultivars; and temperate compared with tropical grasses.

Studies with separated leaf and stem fractions have shown that sheep and cattle eat a greater quantity of leaf than stem of similar digestibility, and that the stem fraction is retained in the rumen for longer than the leaf fraction (Minson, 1982).

Although there are examples of the intake/digestibility relationship holding over a range of pasture species or plant communities (e.g. Armstrong, Common and Smith, 1986), in some instances the relationship has been found to vary between species or cultivars and this may be due to variation in the degree of leafiness (Minson, 1982).

In general, as grasses mature the proportions of stem and of fibre increase and both digestibility and herbage intake decline (Laredo and Minson, 1973; Minson, 1982). Hence, if tropical and temperate grasses are compared at a digestibility of 0.60, the intake of the tropical grass, which is immature and leafy at this digestibility, will be greater than that of the mature, stemmy temperate grass (Minson, 1982).

The bulk density of the feed has also been shown to affect intake (Peterson, Baumgardt and Long, 1974) as has the DM content. Clearly, any dilution of the feed, whether with air or water, has the potential to reduce DM intake. Several reviewers comment on a positive relationship between DM intake and the DM content of the forage (Arnold, 1964; Stobbs, 1975a; Minson, 1982), but there is no general agreement about the range of DM contents over which this relationship holds and indeed Holmes and Lang (1963) concluded from their experiments that DM intake was not likely to be restricted by either a high internal water content or rain water on the leaf surface.

Whilst the literature indicates that herbage intake in the grazing ruminant is influenced by a complex array of factors, the behavioural control of intake, being responsive to sward canopy structure, remains of central importance. By altering its ingestive behaviour, the animal attempts to maintain an adequate level of intake despite any deterioration in sward conditions.

Sward canopy structure

Before discussing the effects of sward canopy structure on ingestive behaviour, it is necessary to consider which measures of canopy structure are relevant to the animal.

Herbage mass is "an instantaneous measure of the total weight of herbage per unit area of ground, preferably measured to ground level" whereas canopy structure is "the distribution of, arrangement of, and interrelationships between the various components of the canopy" (Thomas, 1980). The term sward canopy structure is used in this thesis to cover measures of sward bulk density, tiller density, sward height, species composition and the vertical distribution of the bulk density of the sward and its morphological components.

Arnold and Dudzinski (1966) considered that herbage mass was "only a crude summation of the pasture conditions" although in many early experiments only herbage mass, and perhaps sward height and herbage digestibility, were measured. The inadequacy of these measurements as descriptions of vegetation as it is perceived by the grazing animal has also been commented on by Arnold and Dudzinski (1969), Stobbs (1975a), Baker (1976), Hodgson (1977, 1982a, 1985a) and Owen-Smith (1982). Furthermore, it is very difficult to isolate the independent effects of canopy structure variables, such as height and density, from each other, from herbage mass, and from the nutritive value or digestibility of the sward (Allden and Whittaker, 1970; Stobbs, 1975b; Hodgson, 1977, 1979a, 1982a; Freer, 1981; Black and Kenney, 1984). All these sward characteristics tend to vary together in relation to the maturity of the sward, and their effects on herbage intake are thought to be additive (Hodgson, 1979a). The dynamic nature of the sward is a further complication (Hancock, 1952; Treacher and Gibb, 1978; Freer, 1981; Hodgson, 1981a).

More sophisticated canopy structure measurements have, however, been made in recent years, with the development of point quadrat and stratified clip techniques to measure the distribution of herbage material vertically through the sward profile (Stobbs 1973b, 1975b; Chacon and Stobbs, 1977; Hodgson, 1981a, Forbes, 1982a). Stobbs (1973b, 1975b) pointed out the marked changes in bulk density, morphological composition and nutritive value in moving down through the sward canopy of tropical grasses. He emphasised (Stobbs, 1975b) the importance of measuring sward characteristics in the surface strata which are most accessible to the grazing animal, rather than measuring average conditions for the whole sward. However, Hodgson (1983) cautioned that animals do not necessarily concentrate their grazing in the surface strata and ideally animal responses should be related to detailed descriptions of the structure of the whole profile. Clearly, the stratum of greatest importance is that which is grazed, but it must be considered within the context of the whole canopy.

Grazing and ingestive behaviour

Grazing is "the defoliation by animals of rooted plants in the field" and the process involves searching for, prehending (grasping) and ingesting plant material (Hodgson, 1979b). Milne, Hodgson, Thompson, Souter and Barthram (1982) considered grazing to comprise first site selection (choice of location) then bite selection (choice of particular plant components). In mixed species swards, bite selection might also involve choice of particular plant species.

Hodgson (1986) described the typical grazing animal as moving steadily forward with the head swinging from side to side in front of the forelegs. Herbage is gathered by the lips which are thin and mobile in sheep, but thicker, wider and relatively immobile in cattle which also use their protractile tongue to gather herbage (Grant, Suckling, Smith, Torvell, Forbes and Hodgson, 1985) unless the vegetation is too short (Arnold, 1981). In sheep, the herbage is gripped between the dental pad and lower incisors and either torn off by a jerk of the head (Arnold, 1981; Hodgson, 1986) or bitten off (cut) (Arnold, 1981; Holmes, 1980). Cattle may also grip herbage between the dental pad and lower incisors (Chambers, Hodgson and Milne, 1981; Hodgson, 1986) or between the tongue and lower incisors (Hafez and Schein, 1962; Holmes, 1980; Van Dyne et al, 1980; Chambers et al, 1981) before pulling or tearing the herbage off, often with a jerking movement (Holmes, 1980).

Vegetation characteristics will influence many facets of the grazing process: the rate and direction of movement of the animal in its initial appraisal of the herbage; the rate of biting; the number of bites between successive swallows; the size and discreteness of individual boli; and the amount of chewing before swallowing (Hodgson, 1986). Freer (1981) considered that the number of masticatory bites is likely to reflect the maturity of the ingested herbage.

It is generally considered that sheep can graze closer to the ground than cattle, due to the structure of the lower jaw (Hafez and Schein, 1962; Van Dyne _et al_, 1980) and the cleft upper lip of the sheep (Van Dyne _et al_ 1980). Hafez and Schein (1962) considered that sheep can graze virtually at soil level, while cattle can only graze to within approximately 1.2 - 1.5 cm of the soil surface (Hafez and Schein, 1962; Hafez, 1966; Van Dyne _et al_, 1980).

The importance of sward attributes in determining the grazing animal's intake and performance has undoubtedly long been appreciated by observant farmers and stockmen. In an early document, Anderson (1797) described various grazing habits of cattle and highlighted the importance of grazing fresh vegetative regrowth and of controlling sward height in order to increase output from the grazing system (see introductory quotation preceding p1).

In the 1920s, various experiments examined grazing behaviour in terms of time spent grazing, ruminating and resting, and from the 1930s onwards estimates of herbage intake were attempted, mainly for dairy cows. Johnstone-Wallace and Kennedy (1944) examined the intake of beef cattle and concluded that a large intake was only possible in favourable grazing conditions, due to the time and effort required in harvesting herbage with the mouth - a relatively small harvesting apparatus. Hancock (1952) first mentioned that grazing time (the length of time spent grazing each day), bite rate (the number of bites per minute) and bite weight (the weight of herbage ingested per bite, often termed bite size or intake per bite) combine to give daily herbage intake, and this approach was subsequently used by Allden (1962) and Allden and Whittaker (1970). Two other expressions can be derived from these variables; the rate of intake (the product of bite weight and bite rate) and the total number of daily bites (the product of bite rate and grazing time). Thus:

$$\text{Daily herbage intake} = \underbrace{\text{bite weight} \times \text{bite rate}}_{\text{rate of intake}} \times \text{grazing time}$$

$$\text{bite weight} \times \underbrace{\text{bite rate} \times \text{grazing time}}_{\text{total daily bites}}$$

Obviously bite rate in this context should be a measure of those jaw movements which sever the herbage (referred to hereafter as "harvesting bites" or just "bites") and should not include jaw movements associated with the initial gathering of herbage and its subsequent manipulation into the back of the mouth before swallowing ("manipulatory bites").

This approach to studying herbage intake through ingestive behaviour is rather mechanistic and relies on the expression of continuous variables as simple means or totals, but it has proved to be very useful and has formed the basis of most of the recent investigations into the effect of sward canopy structure on herbage intake (Hodgson, 1982a, 1985a).

In describing the various ingestive behaviour variables, attention will be concentrated on how they are influenced by herbage mass and sward canopy structure. Methods and equipment used to measure ingestive behaviour have been reviewed by Hodgson (1982b), Penning (1983) and Anderson et al (1985). Other aspects of ingestive behaviour have been reviewed by Stobbs (1975a), Hodgson (1977, 1982a and b, 1983, 1985a, 1986), 't Mannetje and Ebersohn (1980) and Arnold (1981).

Bite weight

On temperate sown swards, the normal range of variation in bite weight is approximately 11-400 mg OM (0.4-2.6 mg OM kg LW^{-1}) for sheep, compared with 70-1610 mg OM (0.3-4.1 mg OM kg LW^{-1}) for cattle (Hodgson, 1986). Bite weight is most commonly measured directly, using oesophageal fistulates and dividing the weight of dried extrusa by the number of bites taken; or indirectly, by dividing the intake over a period of time by the corresponding number of bites taken. The former method tends to give a slightly higher estimate of bite weight than the latter (Jamieson and Hodgson, 1979a and b; Forbes, 1982a) and their relative merits are discussed by Hodgson (1982b). Unfortunately, in work by Stobbs (1973a and b, 1974a, 1975b), Stobbs and Hutton (1974), Chacon and Stobbs (1976, 1977), Chacon, Stobbs and Sandland (1976), Chacon, Stobbs and Dale (1978), Hendricksen and Minson (1980) and Ludlow, Stobbs, Davis and Charles-Edwards (1982), bite weight was calculated by dividing extrusa weight either by the total number of harvesting and manipulatory bites or by the number of harvesting bites plus manipulatory bites taken with the head down, instead of just the harvesting bites. True bite weight was therefore underestimated by an unquantifiable and probably variable amount, although Stobbs (1975b) estimated that the error in his work was unlikely to be more than 5%.

Jamieson and Hodgson (1979b) found that under conditions of continuous stocking lambs had a greater bite weight per kg live weight than calves. Forbes (1982a) obtained a similar result for mature sheep and cattle grazing indigenous hill swards, when comparing mean values per year estimated by the indirect method previously mentioned. Overall, however, he found that on a live weight basis sheep and cattle bite weights estimated using fistulates did not differ significantly; nor did they differ when sheep and cattle grazed down sown swards (Forbes and Hodgson, 1985a).

When expressed on a metabolic live weight basis, bite weight is greater for cattle than for sheep (Jamieson and Hodgson, 1979b; Forbes and Hodgson, 1985a) and animal size can be an important determinant of bite weight (Illius, 1986). Following Clutton-Brock and Harvey (1983), Illius and Gordon (1987) modelled the relationship between body weight and bite weight over a range of ruminant species. On short swards small animals obtain a higher proportion of their metabolic requirements than large animals because the depth of a bite is relatively less limited. On very short swards, the only unrestricted bite dimension lies along the biting surface formed by the incisors, and consequently bite weight is proportional to incisor width, which scales as body weight$^{0.36}$ among ruminants. Lastly, when herbivores select small discrete food items, such as leaf tips, bite weight may be unrelated to body weight, and could even be negatively related where a larger mouth is a disadvantage mechanically.

Modification of bite weight is the primary animal response to changing sward structure (Hodgson, 1986) and was first studied in any detail in Australia in the 1970s. Stobbs (1973a and b, 1975b) and subsequently Ludlow et al (1982) studied the bite weight of oesophageal fistulated cows grazing tropical grass or legume swards with a range of canopy structures created by using different forage species, regrowth periods, and fertiliser and plant growth hormone pre-treatments. It was concluded from these experiments that the most important sward characteristics influencing bite weight were sward bulk density, leaf bulk density and leaf content, these variables all having a positive effect. In Stobbs (1975b), all quoted correlation coefficients between bite weight and sward measurements were higher when the sward measurement in question reflected conditions in the top two strata of the sward rather than mean conditions for the whole sward, but it would appear that the suggestion that cows were grazing these particular layers was based on a comparison of the leaf and N contents of the sward and diet, rather than on any observation of animal activity or comparison of sward height before and after grazing.

Moreover, although Stobbs (1973a and b; 1975b) did not consider that sward height had an important effect on bite weight, and Ludlow et al (1982) found the relationship to be negative, the data quoted by Stobbs (1973a, 1975b) would indicate a positive relationship in at least one of the experiments described in each paper.

A further complication in most of these trials was that sward treatments resulted in differences in digestibility and N content, and these quality factors may have influenced bite weight.

The confounding of sward structural and nutritional characteristics, and the fact that animals are presumably more likely to respond to sward conditions in the grazed stratum than to average conditions in the whole sward, may explain why the bite weight/herbage density relationship was not very consistent between the various grazing trials described by Stobbs. Bite weight was shown to increase with increases in mean sward bulk density up to approximately 0.87 mg DM cm^{-3} (Stobbs, 1975b) or even 2.69 mg DM cm^{-3} (Stobbs, 1973a), or alternatively to fall sharply above density values of 0.32-0.34 mg DM cm^{-3} (Stobbs, 1973b). Relationships with density in the surface stratum were more consistent; bite weight on both Setaria (Setaria anceps) and Rhodes grass (Chloris gayana) swards increased up to surface stratum densities of 0.22-0.32 mg DM cm^{-3} (Stobbs, 1973b, 1975b). With further increases in density, however, bite weight either remained constant (Stobbs, 1975b) or subsequently fell sharply as the sward matured (Stobbs, 1973b). It seems likely that factors such as sward height, leafiness and digestibility would have confounded this relationship, and firm conclusions on bite weight response patterns cannot be drawn.

In addition to the references already quoted, Chacon and Stobbs (1976) and Hendricksen and Minson (1980) also attributed variation in bite weight on tropical or subtropical swards more to variation in sward bulk density and leaf content than to sward height. Again, however, the data presented indicated positive relationships between bite weight and sward height or herbage mass, and such relationships were also found on the tropical and subtropical swards studied by Chacon et al (1978), Forbes and Coleman (1985) and Moore, Sollenberger, Morantes and Beede (1985).

Unlike tropical swards, on temperate swards height rather than density is generally considered to have the dominant influence on bite weight. Positive, and usually linear, relationships between bite weight and sward height or herbage mass (or green herbage mass) were found by Allden and Whittaker (1970), Hodgson and Milne (1978), Jamieson and Hodgson (1979b), Bircham (1981), Hodgson (1981a), Hodgson and Jamieson (1981), Forbes (1982a), Forbes and Hodgson (1985a), Penning (1986) and Phillips and Leaver (1986).

In seeking to explain these differences between tropical and temperate swards, it is recognised that tropical swards generally have a lower bulk density and higher stem content than temperate swards (Stobbs, 1973b, 1975a; Dirven, 1977; 't Mannetje and Ebersohn, 1980; Mott, 1983). A comparison of sward conditions in the major tropical and temperate experiments investigating bite weight in cattle (Hodgson, 1983) indicated only slight differences in most canopy structure variables but the bulk density of green leaf in the surface stratum of the tropical swards was on average only about half that of the temperate sown swards (Table 1). This might explain the importance of the leafiness and density variables on the tropical swards.

Table 1

The bite weight of cattle and characteristics of the tropical and temperate swards on which it was measured (After Hodgson, 1983)

	Tropical swards[a] (n=31)		Temperate swards sown[b] (n=32)		Temperate swards indigenous[c] (n=12)	
	Mean	s.e.	Mean	s.e.	Mean	s.e.
Bite weight (mg OM kg LW^{-1})	1.0	0.13	2.0	0.17	0.7	0.06
Herbage mass (t DM ha^{-1})						
Total	4.1	0.38	4.0	0.34	6.4	1.36
Green leaf	2.0	0.21	1.5	0.11	1.2	0.14
Proportion of green leaf	0.5	0.03	0.5	0.03	0.2	0.03
Surface height (cm)	39	5.0	34	3.7	26	3.5
Mean bulk density (mg DM cm^{-3})						
Total	1.2	0.14	1.3	0.06	3.0	0.64
Green leaf	0.5	0.05	0.6	0.05	0.5	0.07
Surface stratum bulk density (mg DM cm^{-3})						
Total	0.2	0.04	0.3	0.03	-[d]	-
Green leaf	0.08	0.013	0.15	0.012	-	-

a Stobbs (1973a and b, 1975b), Chacon and Stobbs (1976), Hendricksen and Minson (1980) and Ludlow et al (1982)

b Combellas (1977), Jamieson and Hodgson (1979a), Hodgson and Jamieson (1981) and Forbes (1982a)

c Forbes (1982a)

d Not possible to calculate the mean and s.e., but surface stratum total bulk density reported in Forbes (1982a) to range from 0.003 to 0.4 mg DM cm^{-3}

The lower bite weight of cattle on tropical compared with temperate sown swards (Table 1) was probably also a reflection of the contrasting surface strata densities. Bite weight might also be affected by differences in the mechanical properties of tropical and temperate grasses, but no reliable data are available.

Stobbs and Hutton (1974) compared the bite weight of cattle on tropical grasses and on immature oats (Avena sativa) which had a low stem content and long leaves. Bite weight ranged from 130 to 490 mg OM on the tropical grasses but from 470 to 810 mg OM on the temperate cereal. The authors commented that on leafy swards bite weight was governed largely by the amount of herbage the cow could harvest with each sweep of the tongue and was therefore related to the availability of leaf and leaf length.

The apparently contradictory results obtained in experiments with tropical and temperate swards, and the considerable problem of isolating the independent effects of sward height and density which are normally negatively correlated both within and between swards, illustrate the complexity of this area of research. The Experimental section of this thesis describes one recent approach to examining in detail the animal's bite weight responses to variations in sward height and density (Experiment 2). While this work was underway, an account of a second approach, using artificial pastures, was published by Black and Kenney (1984) in Australia. Since the two approaches are in many ways complementary, the trials run by Black and Kenney (1984) are not discussed in the Literature Review but are considered together with Experiment 2 in the Discussion section of that experiment. Both experiments measured bite dimensions, and the background to these measurements is discussed below.

Bite dimensions

The three bite dimensions of interest are:

a. bite depth, the difference between the pre-grazing sward surface height and the height of the grazed herbage after one bite has been taken;

b. bite area, the horizontal area encompassed by the bite;

c. bite volume, the product of bite depth and area. Bite volume is the volume occupied in the sward by the herbage prehended at a bite.

The bite dimensions are illustrated in Figure 3. By definition, bite weight is the product of bite volume and the bulk density of herbage in the grazed stratum. Figure 4 shows the interrelationships between these various measurements, the other ingestive behaviour variables, and herbage intake.

Prior to 1984, bite dimensions had not been systematically investigated in grazing experiments and little was known about these measurements. Their importance, however, is evident since a consideration of bite weight as the product of bite volume and herbage density explains the positive relationship between bite weight and herbage density noted in the tropical experiments. The apparent absence of a bulk density effect on temperate swards is probably due to the dominant effect of correlated changes in sward height (Hodgson, 1983).

Before discussing bite depth, area and volume in more detail, it should be pointed out, as by Hodgson (1985a) that while individual bites can be described in terms of bite dimensions on uniform, vegetative or early reproductive swards where animals graze largely unselectively from the surface down, this may not be the case on all swards. On more mature, taller or more complex swards where animals tend to sever individual leaves or groups of leaves and draw them into the mouth for chewing, measurements such as bite area and herbage bulk density may

Figure 3

The three bite dimensions; bite depth, bite area and their product, bite volume

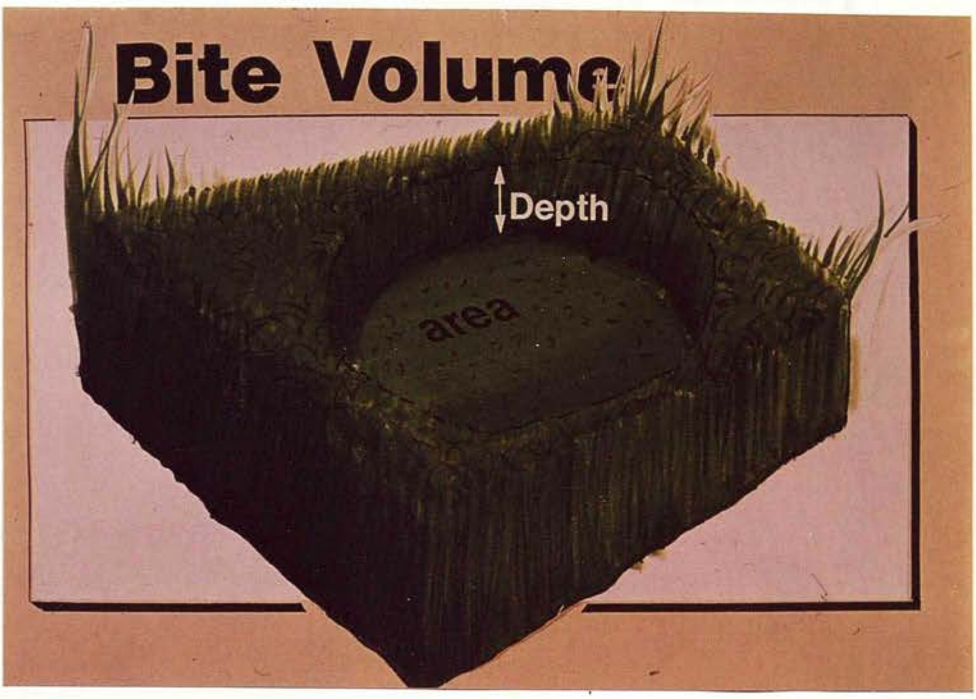
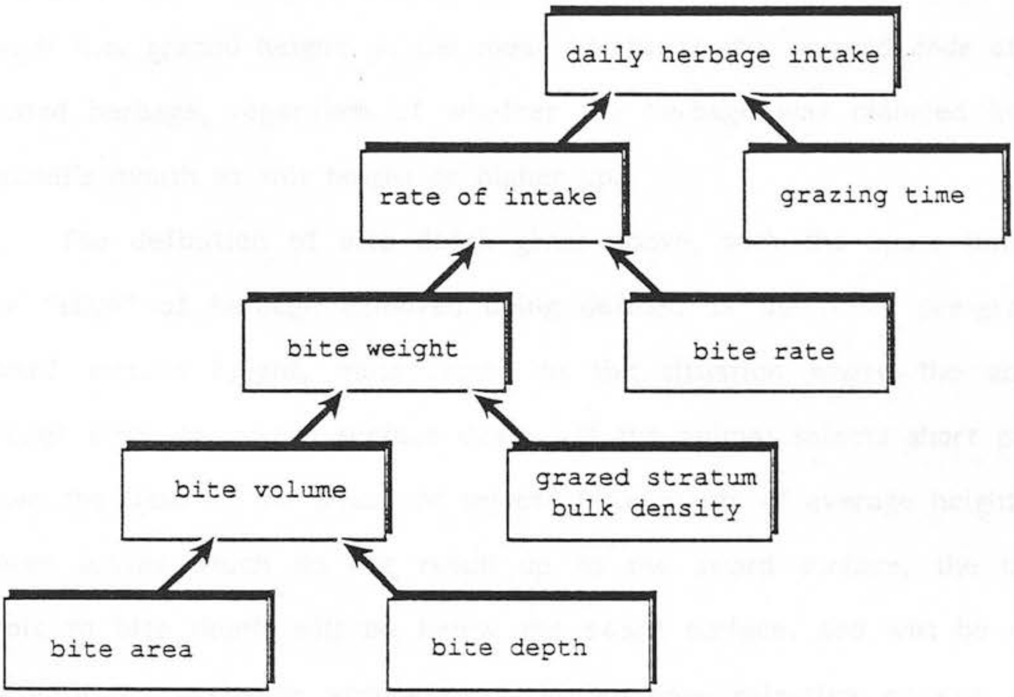


Figure 4

The components of daily herbage intake



be less relevant than the dimensions of individual leaves and their ease of prehension and manipulation for swallowing (Hodgson, 1983; 1985a).

Bite depth

Bite depth is not necessarily limited by the dimensions of the buccal cavity, since both sheep and cattle frequently grip leaves or tillers and tear them off before drawing them into their mouths (Hodgson, 1982a). Clearly after a bite is taken the lower limit to bite depth (i.e. grazed height) is the mean height of the severed ends of the rooted herbage, regardless of whether the herbage was clamped in the animal's mouth at this height or higher up.

The definition of bite depth given above, with the upper limit to the "slice" of herbage removed being defined as the mean pre-grazing sward surface height, must relate to the situation where the animal grazes from the sward surface down. If the animal selects short plants from the base of the sward or selects from plants of average height the lower leaves which do not reach up to the sward surface, the upper limit to bite depth will be below the sward surface, and will be more difficult to estimate accurately. In extreme selective grazing, bite depth as defined above - like bite area and herbage bulk density mentioned earlier - may not be a meaningful statistic.

The consensus of opinion appears to be that cattle generally graze a sward from the surface down (Lane and Holmes, 1971; Stobbs, 1975a, 1977a). Sheep may behave similarly (Arnold, 1964; Milne et al, 1982; Barthram and Grant, 1984) but L'Huillier, Poppi and Fraser (1986) found that the distribution of grass green leaf determined which strata were grazed. Sheep grazed apparently indiscriminantly at the surface of all swards with a high green leaf content in the upper strata, but grazed largely in the basal 3 cm of an 18 cm tall sward which had a very high content of dead flowering stem, with green herbage only in the basal stratum.

In describing the results of a series of grazing trials on contrasting temperate pastures, Grant and Hodgson (1980) and Hodgson and Forbes (1980) quoted figures for the most frequent depth of grazing for mixed-stocked sheep and cattle. These data were obtained from estimates of the depth of head insertion into the sward, and indicated that on a perennial ryegrass (Lolium perenne) sward (surface height approximately 11 cm), both sheep and cattle concentrated their grazing in the top 5 cm of the sward, whereas on a Nardus-dominant community (surface height 25-35 cm) sheep tended to graze at a depth of 10-25 cm and cattle at a depth of up to 15 cm.

Forbes (1982a), Milne et al (1982) and Barthram and Grant (1984) estimated grazed depth from detailed sward measurements. It should be noted that grazed depth estimated in this way may reflect several successive bites down the sward profile, in which case it does not equate with bite depth as defined earlier. However, Forbes (1982a) considered that true bite depth was probably measured in his experiment because of the short (15-20 min) grazing period allowed, and because of evidence from visual observations. In his trials on small plots representing a wide range of pasture species, sheep and cattle appeared to graze from the surface of the leaf stratum down. There was a strong positive linear relationship between grazed depth - or strictly the length of leaf removed - and the pre-grazing leaf length. Grazed depth ranged from 0.3 to 14.4 cm at mean leaf lengths of 8.5 and 25.0 cm respectively for cattle, and from 0.3 to 11.9 cm at mean leaf lengths of 10.4 and 31.7 cm respectively for sheep.

Barthram and Grant (1984), working with much shorter (1.7-4.8 cm) perennial ryegrass swards grazed down over 24 days by sheep, found a strong indication that grazed depth was limited by the pseudostem height (height of the uppermost ligule). Grazed depth ranged from 0.5 to 2.5 cm, usually within a few mm of pseudostem height (G.T. Barthram, personal communication). Barthram and Grant (1984) pointed out that when the pseudostem acts as a barrier to defoliation, the reduction in bite depth is likely to limit bite weight and consequently also the daily herbage intake.

When sheep were grazed for short periods on taller (approximately 6-19 cm) mixed swards of perennial ryegrass and white clover (Trifolium repens), Milne et al (1982) found that both grazed depth and grazed height were positively and linearly related to surface height. Grazed depth on these taller swards ranged up to approximately 6.5 cm and was not considered to be restricted by pseudostem material.

Bite area and volume

Prior to 1984, no reliable estimates of either bite area or bite volume were published. Morris (1969) deduced that continuously-stocked lambs tended to graze patches of herbage up to an area 16 x 16 cm before moving to a different place in the sward, but this was an estimate of grazed area rather than bite area. Grazed area is likely to result from several adjacent bites in a horizontal plane, just as grazed depth may result from several successive bites in a vertical plane.

Hodgson (1981a), discussing the results of strip-grazing experiments using calves, pointed out that since bite weight declined as sward height fell and the animals grazed strata of increasing bulk density, bite volume must have declined very rapidly indeed. Bite volume, however, was not measured.

Bite area and volume are likely to be directly related to mouth dimensions within animal species, although both bite dimensions will vary with inter-specific differences in the use of the lips and tongue to gather herbage (Hodgson, 1983). Sheep can remove individual leaves from a plant, and although cattle can also do this in some circumstances, they more often sweep an area of herbage into the mouth with the tongue (Hodgson, 1982a).

Whereas on very sparse swards the number of leaves and stems prehended at a bite is probably limited by the maximum bite area (Hodgson, 1985a), on dense swards the structural strength of the herbage may be a deciding factor (Hodgson, 1985a; Hughes, unpublished). This is discussed next.

A certain amount of confusion has surrounded the measurement of the mechanical properties of plants, due to the misuse of terminology. The tensile properties of plant material relate to its behaviour under stretching. When a leaf is gripped then stretched by applying an increasing load or force (mass x acceleration) until it breaks by ripping, its tensile strength is indicated by the stress (force per unit cross-sectional area) which is required to break it. The stiffness of the material is the stress divided by the strain, where the strain is the relative extension to produce that stress. Stiffness is estimated from the first, linear portion of the stress-strain curve (Vincent, 1983) and not at the breaking point.

Unlike tensile strength or stress, shear strength or stress is a measure of the tendency for one part of a solid to slide past the neighbouring part. It is calculated from the shear force per unit area being sheared. The force required to sever a leaf by cutting is its shear force.

In much of the work on tensile and shear strength of grass leaves, various authors have expressed these properties in non-standard terms which are neither absolute nor, in many cases, comparable with other work (for example, Beaumont, Stitt and Snell, 1933; Evans, 1964, 1967a and b; Wilson, 1965; Theron and Booysen, 1966, 1968; Martens and Booysen, 1968; Hendricksen and Minson, 1980; Rogalski and Kozlowski, 1981; Rogalski and Domanski, 1983). Bearing in mind these limitations, comparisons within experiments suggest - as might be expected - that the tensile force required to break grass leaves is greatest at the leaf base and least at the tip (Kneebone, 1960; Evans, 1967a; Martens and Booysen, 1968). In addition, younger leaves (either leaves on plants at an earlier stage of growth or leaves from the tip of the culm) have a lower tensile strength than older leaves (Kneebone, 1960) and this property varies between grass species (Evans, 1967a; Martens and Booysen, 1968; Theron and Booysen, 1968).

Bignall (1984) measured the standard tensile properties of the flag leaf of seven temperate grass species and found significant differences between species in both breaking strength and stiffness. Breaking strength and stiffness were positively related. These two properties are a direct function of the amount of sclerenchyma present (Vincent, 1982).

In one of the few experiments in which shear forces were measured, Hendricksen and Minson (1980) found that cattle had a strong preference for the leaf rather than the stem of the subtropical forage legume Lablab purpureus, and this preference was considered to be assoicated with the higher shear loads required to harvest the stem. It was also suggested that coarse stems might have been avoided because they would required considerable mastication before swallowing. The consequence of the aversion to stem - for whatever reason - was that as the crop was grazed down and available leaf declined, bite weight and hence herbage intake fell sharply (Hendricksen and Minson, 1980).

Neither the tensile nor the shear forces required to sever grass stem appear to have been measured, although it seems reasonable to expect higher values than for laminae, particularly for mature stems.

Before discussing in more detail the likely implications for the grazing animal of variations in the structural strength of herbage, the relative importance of tensile and shear forces in the grazing process is assessed.

Vincent (1982) suggested that large grazers, such as cattle, do not use the teeth for cutting, but break clumps of grass in tension by pulling vertically, often twisting the grass at the same time. He later commented (Vincent, 1983) that grazing sheep, horses and geese probably introduce a compression crease into the lamina by pulling it through a sharp angle. The notching of the sclerenchyma bundles makes fracture easier, but only a few laminae may be creased at each bite.

Therefore, tensile forces appear to assume a greater importance than shear forces in the severing of herbage by cattle, but both types of force are important for sheep. Presumably a vertical plucking action would sever herbage by predominantly tensile forces, whereas if the head is jerked backwards and forwards parallel to the ground then shearing forces also come into operation. Shearing forces are also involved in mastication by the molars prior to swallowing (Hughes, unpublished).

Sward canopy structure is likely to influence the methods employed by the grazing animal in harvesting its food. The only detailed account in the literature appears to be for barnacle geese (Bignall, 1984). When geese grazed different grasses in boxes on a force platform, they appeared to distinguish between long and short grasses, and between young and old grasses, and alter their grazing method accordingly. Factors which varied included the amount of material gathered per bite, whether a shearing or plucking action was used, the velocity and rotation of the head, and the direction of the forces severing the grass.

Owen (1976, 1978) postulated that geese might select individual grass species or plant parts on the basis of their mechanical properties, either by feeling the plant unit and then accepting or rejecting it (possibly on the basis of its stiffness?), or by using a standard pull which allowed some leaves to slip through the bill while others were broken off and ingested. Since mechanical properties of herbage are usually correlated with nutritive value and digestibility, it is possible that mechanical properties are used as an indicator of quality (Owen, 1976, 1978). However, Bignall (1984) stated that geese do not appear to test the vegetation before they eat, and she considered it more likely that visual or olfactory, rather than mechanical, cues are used. She also pointed out that at high peck rates (up to 120 pecks min^{-1}) there is little time to test the vegetation, and that it is unlikely that a blade will be so strong that it slips through the bill unbroken - although if too many blades are gathered they may not all break.

It has been suggested that for ruminants grazing on reasonably dense swards where plants are clumped, the number of plant units severed at a bite - and hence bite area, bite volume and bite weight - may be limited by the effort required to sever the herbage (Hodgson, 1985a; Hughes, unpublished). The theory presupposes that there is a set limit to force expenditure per bite, which Hughes (unpublished) called the summit force per bite. Evidence to support this is drawn from the experiments of Chambers et al (1981) who found that there were only relatively small variations in the rate of head acceleration during biting, both within and between swards, for sheep and for cattle. Only one or two experimental animals were used, but the data suggested that a relatively constant force was applied by the cow or sheep in severing each mouthful of herbage (in contrast to the data for geese; Bignall, 1984).

The theory for ruminants predicts that, other things being equal, bite area will decrease with increases in the number of plant units per unit area, their tensile strength and/or their cross-sectional area. Thus, biting deeper into a dense sward might be expected to lead to a reduction in bite area (Hughes, unpublished). The apparent preference of the grazing ruminant for leaves in the surface stratum of a vegetative sward might reflect their low tensile strength as well as their accessibility, but instantaneous assessments of nutritive value would seem unlikely (Hughes, unpublished).

When bite depth is limited by the presence of pseudostem (Barthram and Grant, 1984), this could be because of the close proximity of dead material in the base of the sward, or because pseudostem is more difficult to gather and grip than leaves, or because the tensile force required to harvest pseudostem is likely to be much greater than for leaf (Hughes, unpublished).

To sum up current knowledge about bite weight in grazing animals: this is clearly a very important behavioural variable since changes in bite weight are the primary response to changing sward canopy structure. Bite weight has been found to respond positively to either sward surface height or bulk density, the former response being observed mainly on temperate swards and the latter on tropical swards. Of its component bite dimensions, bite depth appears to be positively related to surface height and may be limited by pseudostem height on short vegetative swards, whilst bite area and bite volume have barely been investigated. It is considered that on sparse swards the number of plant units prehended at a bite is likely to be restricted by the maximum bite area, whereas on dense swards the limiting factor may be the maximum force expenditure per bite (the summit force per bite).

Bite rate

The range in bite rate for sheep and cattle in several experiments on temperate sown swards is given by Hodgson (1986) as 22-94 and 20-66 bites min^{-1} respectively. Higher bite rates have been quoted for cattle (for example Johnstone-Wallace and Kennedy, 1944; up to 90 bites min^{-1}) but it is not clear whether such values include manipulatory bites, as in the work of Stobbs (1974b), Chacon and Stobbs (1976), Chacon et al (1976) and Hendricksen and Minson (1980). In one of the few experiments where ingestive behaviour was measured for sheep and cattle grazing together on a range of swards, Forbes (1982a) found that mean bite rate was not consistently higher for either animal species.

Bite rate has been measured both by a wide range of automatic recorders, which will not be described here, and by manual techniques. Jamieson and Hodgson (1979a) used the "20 bite technique" in which the time taken for 20 bites was recorded by stopwatch, and the records subsequently converted into bites per minute. Each bite was characterised by a short, sharp jerk of the head and the sound of the herbage being severed. A record was discarded if an animal raised its head from the sward before completing 20 bites, and this technique therefore provided a measure of the potential (maximum) bite rate for the particular sward conditions.

Forbes (1982a) and Forbes and Hodgson (1985a) subsequently modified the technique to allow the incorporation of searching time into a record. Recording continued both when an animal walked with the head down whilst obviously selecting herbage, and when the head was lifted while chewing large mouthfuls of herbage in between bouts of biting. A closer estimate of the long-term mean biting rate would have been obtained with this modified technique.

Regardless of the measurement technique, bite rate records should be taken several times a day. Hodgson (1982b) recommended covering at least the major grazing periods of the day, particularly those in the early morning and evening, with repeated observations during grazing periods if possible. This is because in many experiments bite rate has been found to vary between grazing periods (Rodriguez Capriles, 1973; Stobbs, 1974a; Hodgson and Milne, 1978; Forbes, 1982a; Phillips and Leaver, 1986) and to decline within grazing periods (Hancock, 1952; Stobbs, 1974a and b; Jamieson and Hodgson, 1979a).

Allden and Whittaker (1970) found that bite rate in sheep increased steadily as tiller length decreased from 37 cm to 5 cm, although it then fell sharply as tiller length fell to 4 cm. In general, other experiments have confirmed a negative relationship between bite rate and sward height or herbage mass, on both temperate and tropical swards (Arnold, 1964; Chacon and Stobbs, 1976; Jamieson and Hodgson, 1979b; Chambers et al, 1981; Hodgson and Jamieson, 1981; Forbes, 1982a, experiment 3; Milne et al, 1982; Penning, Steel and Johnson, 1984; Moore et al, 1985; Scarnecchia, Nastis and Malechek, 1985; Broom and Arnold, 1986; Penning, 1986; Phillips and Leaver, 1986). Bite rate may also be negatively related to leaf content (Chacon and Stobbs, 1976; Forbes, 1982a, experiment 3 cattle).

An increase in bite rate, reflecting a decline in sward height or herbage mass, has been found to be accompanied by a decrease in the ratio of manipulatory to harvesting bites in sheep (Chambers et al, 1981; Penning et al, 1984; Short, 1985; Penning, 1986) and possibly in cattle (Chambers et al, 1981). Consequently, within each of these experiments the total number of harvesting plus manipulatory bites per minute remained relatively constant, at least for sheep. These observations suggest that bite rate (the number of harvesting bites per minute) may be a direct response to sward conditions rather than a compensatory mechanism for a reduced bite weight (Hodgson, 1986).

Chambers et al (1981) found that the ratio of manipulatory to harvesting bites was consistently greater for sheep than for cattle at any given sward height, presumably reflecting the greater use of the lips by sheep in manipulating herbage.

Rate of intake

Rate of intake, the product of bite weight and bite rate, may range from 22 to 80 mg OM kg LW^{-1} min^{-1} for sheep and 13 to 204 mg OM kg LW^{-1} min^{-1} for cattle on temperate sown swards (Hodgson, 1986). A daily mean value for rate of intake may be estimated by dividing daily herbage intake by grazing time. Alternatively, rate of intake over a short period may be measured directly using oesophageal fistulates; or estimated from the difference in animal live weight before and after a certain time spent grazing, after allowing for faeces, urine and insensible weight losses. The last approach was employed by Allden and Whittaker (1970) who found that the potential intake rate of hungry sheep could be as high as 190 mg DM kg LW^{-1} min^{-1}. More recently, Penning and Hooper (1985) also used this approach, but with more refined techniques, and found that the rate of intake estimates were not significantly different from corresponding values obtained by dividing daily herbage intake by grazing time.

Rate of intake has been found to be positively related to herbage mass or sward height (Arnold, 1964, 1975; Allden and Whittaker, 1970; Chacon and Stobbs, 1976; Hodgson, 1981a; Forbes, 1982a, experiment 3 cattle; Curll and Davidson, 1983; Penning and Hooper, 1985; Penning, 1986). Rate of intake may also be positively related to leaf content and leaf bulk density (Chacon and Stobbs, 1976).

Grazing time

On temperate sown swards, grazing time has been found to vary from approximately 6.5 to 13.5 h d^{-1} for sheep and 5.8 to 10.8 h d^{-1} for cattle (Hodgson, 1986). Whereas Hafez and Scott (1962) and Van Dyne _et al_ (1980) stated that sheep graze for longer than cattle, Arnold (1981) stated that the range in grazing times, from 4.5 to 14.5 h d^{-1}, is similar for both species. Moreover, Forbes (1982a) found that under conditions of mixed stocking on a range of temperate swards there was no consistent difference between grazing times for sheep and cattle.

Diurnal patterns of grazing activity are similar for sheep and cattle (Arnold, 1981). The animal's grazing periods alternate with time spent ruminating and resting, and the duration and to some extent distribution of grazing and ruminating activity may be influenced by sward conditions, grazing management and climatic variation (Hodgson, 1982b). The major grazing periods begin near dawn and again in the evening, ending near to sunset (Arnold, 1981). Grazing time may be limited by fatigue or the demands of other behavioural activities. Rumination may occupy anything from 1.5 to 10.5 h d^{-1} (Arnold, 1981). Longer rumination times are required with poorer quality fibrous herbage (Stobbs, 1975a). Freer (1981) commented that social factors and daylength may also contribute to the reduction in grazing time, although night-time grazing is not uncommon (Arnold, 1981).

Grazing time may be measured manually, usually at five or ten minute intervals; or automatically, usually continuously. The Kienzle vibracorder (Allden, 1962; Hodgson, 1982b) would appear to be the most commonly used automatic recorder. Jamieson and Hodgson (1979b) found a good agreement between grazing time values measured concurrently by vibracorder and by visual observations at ten minute intervals.

Stobbs (1974a) and Stobbs and Hutton (1974) reported that grazing times for cows were, on average, shortest on temperate swards including oats (mean value 7.7 h d^{-1}), and increasingly longer on immature tropical swards, mature tropical grasses and mature tropical legumes (mean values 9.4, 11.3 and 12.0 h d^{-1} respectively). Unfortunately, no details of canopy structure were given.

Grazing time is generally negatively related to herbage mass or sward height (Arnold, 1960b, 1975; Allden and Whittaker, 1970; Chacon et al, 1978; Hodgson and Milne, 1978; Jamieson and Hodgson, 1979b; Forbes, 1982a, experiment 3; Curll and Davidson, 1983; Forbes and Coleman, 1985; Penning and Hooper, 1985; Moore et al, 1985; Scarnecchia et al, 1985; Penning, 1986; Phillips and Leaver, 1986). On particularly short or sparse swards, however, grazing time may start to decline (Arnold, 1964; Chacon and Stobbs, 1976; Hendricksen and Minson, 1980; Bircham, 1981). Forbes (1982a, experiment 3) also found that grazing time for sheep was negatively related to the leaf content of the sward.

Total daily bites

The total number of harvesting bites taken in a day may be measured directly (by automatic recorder) or estimated either from the product of bite rate and grazing time, or from daily intake divided by an independently-derived estimate of bite weight.

There is some uncertainty as to the upper limit to total daily bites. On a temperate sown sward, the grazing sheep may take between 10,000 and 78,000 bites per day, and the grazing cow between 8,000 and 36,000 (Hodgson, 1986) or up to 43,000 (Zoby and Holmes, 1983). On temperate indigenous swards, Forbes (1982a) recorded total daily bites ranging from 20,000 to 49,000 for sheep and from 27,000 to 46,000 for cattle on the same plots. However, Stobbs (1973a, 1974a, 1975a) and Stobbs and Hutton (1974) stated that cows on tropical swards rarely exceed 36,000 bites per day.

The response in total daily bites to changes in sward canopy structure will obviously reflect the combined responses of bite rate and grazing time. Thus there may be a negative relationship between total daily bites and sward height or herbage mass, as in the work of

Jamieson and Hodgson (1979b), or alternatively the total daily bites may increase up to a certain sward height or herbage mass and subsequently decline, as in the work of Chacon and Stobbs (1976).

Interrelationships between sward canopy structure, ingestive behaviour and herbage intake

Thus far, the ingestive behaviour variables have been discussed individually, but it is obviously their combined effect which determines the animal's daily herbage intake. Although on abundant pastures the animal's rate of intake may be limited simply by its rate of mastication and swallowing (Kenney and Black, 1986), sward conditions are usually limiting and bite weight exerts the dominant influence on both rate of intake (Hodgson, 1981a) and daily herbage intake (Chacon and Stobbs, 1976; Forbes, 1982a; Forbes and Coleman, 1984).

As sward conditions become more difficult for the grazing animal, for example if herbage mass or sward height declines, bite weight is directly affected and falls sharply. Bite rate usually increases, but the increase seldom offsets the reduction in bite weight, and consequently the short-term rate of intake falls. The extent to which the animal can increase its grazing time determines how soon daily herbage intake also starts to decline. Eventually, at a low sward height or herbage mass the animal may "give up" and there may be a decrease in grazing time which reinforces the low rate of intake, thus reducing daily herbage intake still further.

This general pattern of ingestive behaviour and intake responses has been found in a wide variety of trials, covering both tropical and temperate swards grazed by sheep and by cattle (Arnold and Dudzinski, 1969; Allden and Whittaker, 1970; Chacon and Stobbs, 1976; Hodgson and Milne, 1978; Jamieson and Hodgson, 1979b; Forbes, 1982a, experiment 3; Penning, 1986; Phillips and Leaver, 1986). In addition, several other experiments have indicated a fall in bite weight and intake with declining herbage mass or sward height, but the responses in bite rate and/or grazing time were non-existent, inconsistent or contrary (Jamieson and Hodgson, 1979a; Le Du, Combellas, Hodgson and Baker, 1979; Hendricksen and Minson, 1980; Bircham, 1981; Hodgson, 1981a; Forbes and Coleman, 1985; Forbes and Hodgson, 1985a). This again suggests that bite weight is more strongly influenced by sward conditions than are bite rate and grazing time.

It has already been mentioned that bite rate, like bite weight, appears to be a direct response to sward conditions. The increase in grazing time which usually accompanies a fall in rate of intake is generally considered to be a compensatory mechanism.

The dominant effect of bite weight on herbage intake is probably due to the fact that in addition to "driving" the animal's intake response, bite weight generally varies to a far greater extent than either bite rate or grazing time. For example, in grazing trials where herbage mass was gradually reduced (Jamieson and Hodgson, 1979a) the daily herbage intake of calves fell by 24% over a six week period and this was accompanied by a 50% drop in bite weight, but only a 22% rise in bite rate and a 14% increase in grazing time. Corresponding figures for lambs were: a 39% fall in intake, 65% fall in bite weight, and increases of 21 and 23% for bite rate and grazing time respectively.

Stobbs (1973a) considered that for cattle the effective upper limit in compensating for a reduced bite weight might be the prehension of a maximum of 36,000 bites per day. He calculated that for a 400 kg cow with a potential DM intake of 3% of body weight, intake might be restricted when bite weight fell below approximately 300 mg OM (0.75 mg OM kg LW^{-1}). However, the concept of this figure being a "critical bite size" (Stobbs, 1973a) is misleading since on the one hand data have already been quoted for total daily bites exceeding 36,000, and on the other hand the intake/bite weight relationship appears to be positive to high values, with no levelling off above any "critical" bite weight (Jamieson and Hodgson, 1979b).

The mean DM intakes of cattle and of sheep, calculated from a wide range of grazing trials, were given as 1.8 and 2.4% of live weight respectively by Van Dyne et al (1980), but as 2.2% of live weight for both species by Skiles and Van Dyne (1983). Leaver (1985) considered that even high-yielding cows normally consume less than 3% of live weight when grazing. Although Forbes and Hodgson (1985a) estimated mean daily intakes of over 4% of live weight for mature, non-lactating sheep and cattle, they considered that such values were either overestimated or a temporary phenomenon, reflecting the management imposed.

The daily herbage intake of the grazing ruminant may be derived from ingestive behaviour measurements or estimated independently using one of three main methods. These are: animal-based techniques such as those relying on the faeces output/diet digestibility relationship (Le Du and Penning, 1982); assessments of animal performance (Baker, 1982); and sward-based techniques (Meijs, Walters and Keen, 1982). The relative merits and drawbacks of the different methods are discussed by these authors.

Daily herbage intake has been found to be positively related to herbage mass and/or sward height in numerous experiments (Johnstone-Wallace and Kennedy, 1944; Arnold, 1964, 1975; Arnold and Dudzinski, 1966, 1967a and b, 1969, 1978; Chacon and Stobbs, 1976; Hodgson, Rodriguez Capriles and Fenlon, 1977; Hodgson and Milne, 1978; Jamieson and Hodgson, 1979b; Hendricksen and Minson, 1980; Baker, Alvarez and Le Du, 1981a; Baker, Le Du and Alvarez, 1981b; Le Du, Baker and Newberry, 1981; Curll and Davidson, 1983; Bircham, 1981; Forbes and Coleman, 1985; Forbes and Hodgson, 1985a; Stockdale, 1985; Penning and Hooper, 1985; Penning, 1986; Phillips and Leaver, 1986). Arnold and Dudzinski (1966, 1969, 1978) also reported a higher intake associated with an increase in the number of leaves per unit area, and in the second of these papers sheep grazing pastures with the same leaf length had higher intakes when the swards were denser. For cattle defoliating swards of a tropical legume (Hendricksen and Minson, 1980) or tropical grass (Chacon and Stobbs, 1976), the mass and proportion of leaf (or green leaf) had a strong influence on herbage intake. In addition, the bulk density of green material (leaf plus stem) was important in the grass swards but not in the legume swards.

It is interesting to consider the shape of the response curves for bite weight, rate of intake and daily herbage intake as sward height or herbage mass changes. Taking sward height first, in the majority of trials, at least on temperate swards, bite weight has been found to be positively and linearly related to height. Moving up a step, rate of intake may have a linear relationship with sward height (Hodgson, 1977, 1981a; Forbes, 1982a, experiment 3 cattle) or the relationship may be asymptotic (Allden and Whittaker, 1970; Penning and Hooper, 1985; Penning, 1986). Consequently, herbage intake may also be asymptotically related to sward height (Penning and Hooper, 1985; Penning, 1986). Although Arnold (1975) found a linear relationship between intake and leaf length, the relationship was asymptotic over a wider range of leaf lengths (Arnold and Dudzinski, 1967a).

Other evidence suggests that the relationships between sward height and bite weight, rate of intake and herbage intake are not necessarily positive. An examination of the data of Stobbs (1973b) indicates that bite weight declined as swards became either very tall or comparatively short. Negative relationships would appear to hold between bite weight and sward height for the tropical swards studied by Stobbs (1973a, experiment 3) and Ludlow et al (1982), where sward density had the dominant influence on bite weight, and height and density were negatively related. Herbage intake on the temperate swards studied by Waite, Holmes, Campbell and Fergusson (1950) was also negatively related to sward height, but this was probably because the longest swards were also stemmy, and probably of lower digestibility.

Sward height and herbage mass tend to be strongly correlated within and often between swards, and both height and mass tend to have a similar influence on herbage intake. The herbage intake/herbage mass relationship has most commonly been described as asymptotic, with intake declining at an increasing rate below a critical mass which has been found to vary between experiments from approximately 1,100 to 4,000 kg DM ha^{-1} for sheep and from 1,100 to 2,800 kg DM ha^{-1} for cattle (Hodgson, 1977). However, in the case of the cattle-grazed swards these figures were underestimated because herbage for mass estimates was cut above ground level. The critical mass may be higher in some cattle-grazed swards. Forbes and Coleman (1985) found that both bite weight and herbage intake approached maximum values at approximately 5,000 kg DM ha^{-1}.

While herbage mass may be best expressed in terms of total herbage DM on swards comprising predominantly green material, it may be more appropriate to relate intake to green herbage DM on pasture containing a seasonally variable amount of dead material (Treacher and Gibb, 1978; 't Mannetje and Ebersohn, 1980) or even to use the mass of the green leaf fraction of the sward if selection for leaf is very strong, as on the tropical legume swards of Hendricksen and Minson (1980). Whatever the terms in which herbage mass is expressed, there is considerable variation in the slope and curvature of the asymptotic relationship, as well as in the critical mass below which intake declines ('t Mannetje and Ebersohn, 1980). This may be due to differences in animal or environmental factors, the herbage species, sward height and density, the proportions and distribution of dead and stem material, and the nutritive value, maturity and digestibility of the herbage (Hodgson and Milne, 1978; 't Mannetje and Ebersohn, 1980; Hodgson, 1986). By minimising the fall in digestibility at high levels of herbage mass, increases in intake may continue to higher levels (Hodgson, 1986). The decline in intake observed by Johnstone-Wallace and Kennedy (1944), Arnold (1964) and Combellas and Hodgson (1979) when herbage mass was high was probably due largely to a decline in herbage digestibility.

Thus far, only domestic sheep and cattle have been considered with regard to ingestive behaviour and intake responses to different sward conditions. There are also many reports in the literature of the responses of a range of wild animal species, and although the necessary measurements have often been made in less controlled conditions than for sheep and cattle, the responses have generally been similar. The animals involved include antelope (Duncan, 1975, reviewed by Jarman and Sinclair, 1980), deer (Skogland, 1980; Trudell and White, 1981; Wickstrom, Robbins, Hanley, Spalinger and Parish, 1984; Hudson and Nietfield, 1985), kangaroo (Clarke and Loudon, 1985; Short, 1985, 1986) and rabbit (Short, 1985).

This section of the Review has highlighted the strong influence which sward canopy structure may exert upon the ingestive behaviour and intake of the grazing animal. Clearly, canopy structure is an important factor to consider in sward management and in plant breeding and selection programmes. The consequences for the sward and for grazing efficiency (herbage consumed divided by herbage accumulated; Hodgson, 1979b) must, however, be considered alongside the consequences for the animal. Normally, factors such as leafiness, a high leaf density, and fine leaves and stems with limited structural tissue improve grazing efficiency as well as herbage intake, but in some circumstances there may be a deleterious effect on grazing efficiency, for example if selective grazing activity is inhibited or herbage losses are increased (Hodgson, 1983).

Plant growth habit can have an important influence on intake. Jackson (1976) reported that cattle had higher intakes when grazed on Italian ryegrass (Lolium multiflorum), which is comparatively erect, than on the more prostrate perennial ryegrass. This was despite a standardisation of herbage mass and herbage allowance, and the fact that the Italian ryegrass had a slightly lower digestibility.

Hodgson (1981b) commented that although a prostrate growth habit and high population of small tillers per plant help the plant to persist under close grazing, an erect growth habit promotes maximum plant growth and usually encourages a higher herbage intake, grazing efficiency and animal performance. The exception to this is the tall tropical sward with a low grazed stratum bulk density which may limit intake. Hodgson (1981b) called for more research to discover the ideal combinations of growth habit and grazed stratum bulk density which optimise herbage intake.

It may be concluded from the literature cited here that the strong influence of bite weight on rate of intake, and hence daily herbage intake, is the key to the animal's grazing responses. Compensating increases in grazing time when bite weight and rate of intake fall are limited. Thus, on temperate swards at least, herbage intake has usually been found to be positively related to either herbage mass or sward height, due largely to the positive effect of these variables on bite weight.

Influence of management and environment

Considered under this heading are the effects of herbage allowance, sward contamination, season - particularly daylength - and weather on the herbage intake of the grazing ruminant.

In general under rotational grazing management, at any given initial herbage mass herbage intake increases with herbage allowance in a curvilinear manner. The asymptote may be approached when the allowance is only twice the maximum intake (Combellas and Hodgson, 1979) or when it is considerably higher (Penning, Hooper and Treacher, 1986). The influence of herbage allowance on herbage intake may be interpreted in terms of its effect upon the rate of change in the structural and nutritional characteristics of the vegetation as the sward is grazed down (Hodgson and Grant, 1985). In a strip-grazing experiment with calves, Hodgson (1981a) found that a simple relationship between the short-term rate of intake and the height of the grazed stratum seemed to explain the effects of herbage mass and herbage allowance on intake, but it cannot be assumed that this is always the case (Hodgson, 1984).

Both Greenhalgh et al (1966) and Stobbs (1977a) pointed out that the opportunity for selective grazing is increased at higher herbage allowances, and Stobbs (1977a) considered that a higher allowance would be required to ensure maximum intake on a tropical sward than on a temperate sward because tropical swards are generally more heterogenous and more selectively grazed. Sheath and Rattray (1985) found that the herbage allowance/herbage intake relationship varied with sward species; legumes and erect-growing grasses in the sward conferred intake advantages especially at low herbage allowances.

Jamieson and Hodgson (1979a) reported that with a reduction in herbage allowance, the intake of strip-grazed calves was depressed due to roughly similar reductions in bite weight, bite rate and grazing time. The lack of the normal compensatory increase in grazing time when the rate of intake of strip-grazed cattle was depressed was also noted by Stobbs (1977a), Le Du et al (1979) and Baker et al (1981a). It might be due to the animals anticipating a move to fresh herbage (Jamieson and Hodgson, 1979a; Le Du et al, 1979).

On continuously-stocked swards, the term herbage allowance is probably meaningless as it fails to take into account herbage growth (Hodgson, 1984). Zoby and Holmes (1983) found that continuously-stocked cattle had a lower intake, with a lower bite weight but higher bite rate and grazing time, at a higher stocking rate (a greater number of animals per unit area of land).

Hodgson and Milne (1978) grazed swards with sheep for twelve-day periods at different initial herbage allowances and commented that the low herbage intakes at low allowances at the end of the grazing period might have been partly due to the adverse effects of fouling, treading and a reduced opportunity for selection. Wade and Le Du (1983) found that the herbage intake of strip-grazed calves was influenced more by the presence of sheep excreta from sward pre-treatments than it was by differences in the sward canopy structure. Herbage intake was higher on previously cut than previously grazed swards, the difference being greater at a lower herbage allowance.

Forbes (1982a) and Forbes and Hodgson (1985b) reported that cattle rejected a herbage fouled by their own species to a greater extent than did sheep. These workers concluded that under mixed grazing a greater proportion of herbage would be available to sheep, giving them a competitive advantage over cattle. Contamination of the sward with urine does not noticeably affect dietary selection (Forbes, 1986) but fungal taint (Jackson, 1976) may have an adverse effect. Nicol, Clarke, Munro and Smith (1976) found that soil contamination might reduce intake of the lower parts of the sward canopy, and on sparse pastures large amounts of soil may be ingested (Young and Corbett, 1972).

Seasonal influences on herbage intake have been reviewed by Reed (1978). Various experiments have indicated higher intakes in spring or summer compared with autumn, despite similar herbage digestibilities. In pen feeding trials these differences in intake may be of the order of 10-20%; in grazing trials even higher. In some experiments animal factors such as stage of maturity may have been involved but in other trials these factors were controlled. Adverse weather conditions, sward contamination and the presence of alkaloids in the herbage might be implicated, but probably the most important potential advantages for spring pastures include a higher herbage mass, higher growth rate, and in ryegrass a more erect growth habit which facilitates prehension. Seasonal changes in herbage composition which result in changes in the rate of breakdown of herbage in the rumen may also affect intake.

Herbage intake may also vary seasonally due to the effects of daylength. This was reviewed by Forbes (1982b; 1986) who stated that under conditions of natural lighting in latitudes where there is a marked annual rhythm in photoperiod, sheep show an annual cycle of daily food intake, with a peak a few weeks after the longest day and a nadir after the shortest day. By providing an "annual" lighting cycle compressed into a six-month period for housed sheep and red deer, Kay (1979) showed that the intake cycle for these species was due to photoperiod rather than to temperature or changes in food quality.

Daylength also affects the periodicity of grazing. Arnold (1981) commented that with shorter days the breaks between grazing decrease, and in mid-winter at latitudes of 20° or more, grazing is almost continuous during daylight. However, significant amounts of food are eaten at night by sheep and cattle and it is most unlikely that daylength affects intake through the length of time food is visible (Forbes, 1982b; 1986). Forbes put forward the hypothesis that a long photoperiod increases intake indirectly, the direct effect of daylength being a stimulation of growth which then stimulates intake. Several references for both sheep and cattle were cited to substantiate the theory, and for example Forbes, El Shahat, Jones, Duncan and Boaz (1979) found that housed lambs fed ad libitum had a 10% higher intake, a higher growth rate and increased gut fill when subjected to a longer artificial lighting "daylength". Forbes (1982b) suggested that the mode of action of the effect of daylength on growth is probably via the eyes to the pineal gland which influences hormonal secretion.

Whereas high ambient temperatures, solar radiation and relative humidity are usually associated with a decrease in intake by the grazing ruminant, cold conditions tend to stimulate an increase in intake unless the animal is subject to severe cold stress (Weston, 1982). Rain does not usually have much effect on grazing activity but grazing ceases in prolonged driving rain, and in colder climates sheep may seek areas sheltered from the wind (Arnold, 1981). Stobbs (1975a) commented that although grazing activity may be reduced during inclement weather, cows compensate by increasing grazing in subsequent periods.

Comparing the housed and the grazing ruminant, the animal at grass has a higher energy requirement as it is more active and is exposed to wind and rain. The energy cost of eating is related to the time spent eating rather than to the weight of herbage consumed, and consequently sparse pasture imposes higher demands for energy on the animal (Forbes, 1986). The total extra energy expenditure by sheep grazing sparse pasture is 25-50% above that of housed sheep and the voluntary intake of grazing animals usually exceeds that of those kept indoors by about this margin (Forbes, 1986). Forbes (1984) commented that animals grazing swards which severely limit herbage intake may find it advantageous not to continue grazing for long periods at a low rate of intake but to reduce their grazing time and therefore reduce their energy requirements.

Animal factors

Hodgson (1977) stated that differences in animal species, age, physiological state and nutritional status may affect potential nutrient intake, rumen capacity and grazing efficiency, thus altering the balance between the controls limiting herbage intake.

Considering first the variation in intake within a ruminant species, Weston (1982) commented that intake may increase during lactation but generally decreases during late pregnancy or with increased body fatness or in disease states. Arnold and Dudzinski (1967a) and Arnold (1975) found that lactating ewes increased their intake by increasing both grazing time and rate of intake, and Tulloh (1966) found evidence of some hypertrophy of the gut to accommodate a larger digesta volume in lactating cows. Arnold and Birrell (1977) reported that adult sheep of comparatively low live weight due to a previous period of under-nutrition had an increased DOM intake, whether expressed in absolute terms or relative to live weight, due to an increase in grazing time or rate of intake.

The patterns of response in herbage intake to variations in sward conditions appear similar for mature cattle in different physiological states with contrasting levels of intake (Hodgson and Jamieson, 1981). Arnold (1975) reported that sheep with different energy demands (due to age, size or reproductive status) maintained the same differences in intake over a wide range of pasture conditions. Similarly, Arnold and Dudzinski (1966, 1967a) found that although the position of curves for the DOM intake/herbage mass relationship varied for dry, pregnant and lactating ewes, the same (asymptotic) shape was maintained for each.

However, Allden and Whittaker (1970) found that on long swards (tiller length approximately 40 cm) lambs had a significantly lower intake rate than yearling sheep, whereas on short swards (tiller length approximately 6 cm) the lambs had the higher intake rate. The same trends were apparent when rate of intake was expressed relative to live weight. Allden and Whittaker (1970) concluded that under conditions of pasture scarcity a small mouth may confer a competitive advantage, but on good pasture a large mouth is advantageous. Unfortunately, grazing time was not measured in this experiment and the modifying effect of grazing time needs to be considered before any conclusion is drawn about the influence of animal class on daily herbage intake.

Zoby and Holmes (1983) compared the intake of cattle of three different sizes and ages under continuous-grazing management. They found that intake per kg live weight increased with animal size, and the smaller animals tended to have a higher grazing time and bite rate but a smaller bite weight. It was concluded that the younger (smaller) cattle were less sensitive than older animals to changes in sward conditions as they were better able to modify grazing behaviour to maintain intake. Hodgson and Jamieson (1981) found that both bite weight and herbage intake when expressed relative to live weight were similar for strip-grazed calves and lactating cows, but that overall the calves had a higher grazing time and lower bite rate.

Sheep of different breeds may differ in the relative extents to which they alter grazing time and bite rate in response to changing pasture conditions (Arnold and Dudzinski, 1969). Shorn sheep subject to cold stress reduce grazing time and eat faster than woolled sheep (Arnold, 1981). Grazing experience may affect intake; Hodgson and Jamieson (1981) found that young inexperienced calves were apparently less competent at achieving high intakes under good sward conditions than were calves which were experienced grazers. Curll and Davidson (1983) found that sheep which were accustomed to swards of low herbage mass had a higher intake, due to a higher grazing time and higher estimated rate of intake, than sheep unaccustomed to those conditions.

Not surprisingly, hunger also appears to affect intake, at least in the short term. Sidahmed, Morris, Weir and Torell (1977) and Jung and Koong (1985) found that the rate of intake of oesophageal fistulated sheep increased when the animals had been fasted for a longer period. Chacon and Stobbs (1977) fasted oesophageal fistulated cows either overnight (for sixteen hours) or for only two hours and bite weight of the longer-fasted cows was subsequently found to be higher on certain pastures. However, fasting was considered to have less influence than sward canopy structure in determining bite weight.

Arnold and Dudzinski (1978) commented that the social use of space, social hierarchy and social facilitation may influence herbage intake, but there are very few quantitative data. Hodgson and Wilkinson (1967) found that the independent effects of live weight and social rank on herbage intake were of approximately equal importance in groups of cattle of the same age. Both Hancock (1952) and Hafez and Schein (1962) listed "inherent individuality" as an animal factor affecting ingestive behaviour and intake. Variation in the length or width of the lower jaw might affect bite weight, bite rate or selective ability (Hafez and Schein, 1962).

Weston (1982) stated that there appears to be no convincing evidence of a general difference in voluntary consumption per kg live weight between sheep, goats, cattle and buffalo. Jamieson and Hodgson (1979b) found that patterns of response in ingestive behaviour and herbage intake were similar for both calves and lambs, although in all animal responses except bite rate lambs appeared more sensitive than calves to changes in sward conditions. Forbes and Hodgson (1985a) found that the bite rate and grazing time of mature sheep appeared to be more sensitive to changes in sward conditions than were these variables for mature cattle, and whereas Jamieson and Hodgson (1979b) could find no evidence that lambs were better adapted to grazing on short swards than were calves, Arosteguy (1982) found that sheep appeared to be better than cattle at maintaining intake on very short swards.

From the evidence quoted, it appears that within an animal species herbage intake may vary with physiological status, degree of fatness, age, size, hunger, grazing experience and social factors. Intake expressed relative to live weight, and the patterns of response in intake and ingestive behaviour to changes in sward structure, appear to be similar for sheep and cattle, but sheep may be more sensitive to changes in sward conditions.

Diet selection

Diet selection by the grazing animal is the removal of some sward component(s) - plants or plant parts - rather than others (Hodgson, 1979b). It is a function of the preferences which would be exhibited between the individual components of a sward were choice unlimited, modified by both the degree to which the characteristics of the vegetation canopy influence the opportunity for selection (Hodgson, 1979b) and by animal-based limitations such as size of mouthparts and mode of biting (Grant et al, 1985).

Hodgson (1979b) drew a strong distinction between the term "preference", which should be used to describe discriminatory grazing activity, and "palatability" which describes the inherent plant characteristic of whether it is pleasant to the taste. Different definitions of palatability have been used in the past, and for example Marten (1969) used it to describe preference or selection. The term "acceptability" is used in this thesis to describe whether the particular combination of characteristics of a herbage - which may include its taste - is, overall, favourable to the animal.

Diet selection in the grazing ruminant is a widely reviewed topic. Various aspects have been discussed by Hafez and Schein (1962), Hafez and Scott (1962), Arnold (1964), McClymont (1967), Marten (1969), Stobbs (1975a), Hodgson (1977, 1982a, 1986), Jarman and Sinclair (1980), Van Dyne et al (1980), Arnold (1981), Freer (1981), Owen-Smith (1982), Minson (1983), Skiles (1984) and Anderson et al (1985). This brief review, after an introduction to the subject, concentrates on a discussion of dietary preferences, the selection of plant species and particularly plant components, the influence of animal factors, and finally how diet selection affects ingestive behaviour and herbage intake.

Selection takes place on a progressively finer scale (Jarman, 1974; Milne, Bagley and Grant, 1979). Depending on how specialised a ruminant species is with regard to its feeding strategy, the animal may simply select a vegetation type, or may go on to select stands of plants or preferred species within the vegetation type, or may also select individual plant components. How far an animal proceeds down this scale of selection varies with the quality of food acceptable to it (Jarman, 1974).

Hodgson (1979b, 1982a) pointed out that differences between the diet and total sward composition are not necessarily indicative of deliberate selection by the animal. Diet composition may simply reflect the composition of the grazed stratum which is grazed unselectively but which has a different composition from the sward as a whole. Clearly, in addition to measuring diet composition a knowledge of the distribution of plant components within the sward canopy is required in order to make an accurate assessment of diet selection (Stobbs, 1975a; Hodgson, 1985b, 1986). Furthermore, it is obviously important that the limits to the grazed stratum be adequately defined.

Although there is an extensive world literature on the botanical composition of the diet of grazing ungulates, including sheep and cattle, there are limits to the conclusions which can be drawn about diet selection. This is because many studies are specific to particular locations and because descriptions of the grazed vegetation are often inadequate (Hodgson, 1982a). Expressions of forage preferences found in the literature range from the percentage of grasses, forbs and shrubs eaten, to rankings by the percentage of different plant species in the diet, to the calculation of various "preference" (selection) indices (Skiles and Van Dyne, 1983; Skiles, 1984). The simplest selection index (sometimes also termed a "ratio") is the percentage by weight of a plant group, species or component in the diet divided by the corresponding percentage in the sward (Hodgson, 1979b; Van Dyne et al, 1980).

In nearly all studies involving wild ungulates, and most of the work on domestic ruminants, selection indices have been calculated using mean sward composition rather than that of only the grazed stratum. Milne et al (1982) compared the proportion of clover in the sheep's diet with that in either the whole sward or grazed stratum of perennial ryegrass/white clover pastures. The apparent selection in favour of clover was much stronger when mean sward composition was used, but there was still some evidence of discrimination when comparing diet with grazed stratum.

Dietary preferences

There is general agreement that sheep and cattle eat leaf in preference to stem, and green (or young) material in preference to dry (or old) material (Arnold, 1981). The material eaten by the grazing ruminant, compared with that on offer, is usually higher in nitrogen, phosphate and gross energy and lower in fibre (Arnold, 1981). However, the animal's motivation in selecting such material is not so easy to determine. Hodgson (1982a) cautioned that most of the evidence on the factors influencing preferences for different plant species and morphological components is derived by inference from uncontrolled field studies, and care is needed in its application.

It has been suggested that the herbage selected may be preferred for its chemical composition per se (Arnold, 1964); or because, due to a lower lignin content, it is easier to harvest (Johnstone-Wallace and Kennedy, 1944; Arnold, 1964, 1981) or easier to chew and swallow, leading to a higher rate of intake (Kenney and Black, 1984); or simply because it tastes better (Arnold, 1981). Glabrousness and succulence are generally favourable plant characteristics, whereas the presence of awns, spininess, hairiness, stickiness, coarseness of texture and unfavourable odour from external glands on the plant usually reduce its acceptability (Heady, 1975). Dead, mature or fungus-infested material is usually rejected (Holmes, 1980). The proportion and distribution of leaf and stem in different plants may affect their relative acceptability (Heady, 1975; Van Dyne et al, 1980) but neither plant growth habit nor factors such as leaf width, texture and flexibility and stem size appear to have a consistent effect (Marten, 1969).

Although in some experiments dietary preferences have been found to be related to particular chemical fractions of the food, Arnold (1981) pointed out that the animal responds to the integrated effects of stimuli from various classes of compounds, and he considered that there was little good evidence to show that preferences are primarily motivated by nutritional wisdom. Like other animals, the ruminant shows hedyphagia - food selection directed at minimising unpleasant or at maximising pleasant (or both) olfactory and other sensations (Arnold, 1981).

The grazing ruminant uses sight, touch in the lips and mouth, taste and smell in diet selection (Arnold, 1981; Owen-Smith, 1982) and the key sense may be taste (Kreuger, Laydock and Price, 1974; Anderson et al, 1985). Kreuger et al (1974) found that preference for different grass species was related primarily to the senses of taste and sight in sheep; olfaction had only a minor role to play. However, Minson (1983) suggested that the most likely explanation for animals disliking dead forage was a difference in odour, and Van Dyne et al (1980) considered it likely that the sense of smell was used to make the initial selection and the sense of taste to continue the selection.

Dietary preferences may change with changing weather and wetness of foliage (Heady, 1975) and selectivity may vary with season (Stobbs, 1975a, 1977b). Van Dyne et al (1980) commented that many wild herbivores are opportunistic, and can compromise their usual food preferences in adverse circumstances. There will be less scope for grazing animals kept under intensive conditions to choose between different vegetation types, and this Review only considers diet selection on a finer scale; the selection of plant species within a vegetation type, and in particular, the selection of plant components within a plant species.

Selection of plant species and components

In general, selection for particular plant species or morphological units increases as within-sward contrasts in plant maturity or physical and biological characteristics increase (Hodgson, 1986). When the variety of potential foods decreases, for example at high grazing pressures, previously rejected species or material may be eaten (McClymont, 1967). Stobbs (1975a) described selective grazing as a dynamic situation; in grazing down a pasture and removing leaf the opportunity to graze leaf is subsequently diminished.

Although there are some differences in levels of herbage intake on swards of different grass species, there is no clear indication of a relationship between the preferences shown for a series of plant genotypes when a choice is available, and the amounts voluntarily consumed when there is no choice (Hodgson, 1977). On a mixed sward, the acceptability of a given species varies with the associated species, and the relative acceptability of individual plants may change as they mature at different rates (Van Dyne et al, 1980). In reviewing the work of Duncan (1975) on the selectivity of topi antelope, Owen-Smith (1982) stated that selection between grass species appeared to be carried out on the basis of structural features rather than plant species per se.

Selectivity normally decreases as forage availability declines (Heady, 1975), and it is also influenced by the distribution of different plant components in both the horizontal and vertical planes, and the degree of mixing of the components (Hodgson, 1982a). Milne et al (1982) found that on perennial ryegrass/white clover swards, sheep appeared to select clover to a greater degree when the proportion in the grazed (surface) stratum was lower, and when swards were taller with a lower grazed stratum bulk density.

In general, the selection of preferred species or morphological components will be easier in an open canopy, such as in an annual grassland or tussock community, where there is relatively easy access to all levels of the sward, than in the closed canopy typical of many temperate short-grass communities where herbage has a high bulk density and the plant units are relatively small (Hodgson, 1982a, 1983). For similar reasons, selection for green material may be greater on a temperate cereal stubble (Mulholland, Coombe, Freer and McManus, 1976) than on a temperate grass sward with a similar green herbage mass (Hamilton, Hutchinson, Annis and Donnely, 1973).

Jarman and Sinclair (1980) reviewed the work of Duncan (1975) and reported that topi selected green leaf from the sward, selectivity increasing linearly with herbage mass. Animals were most selective on grass with long leaves, and least selective when leaf length was short. Selectivity rose sharply when the green leaf proportion in the sward fell below 0.15-0.20, and was highest when the difference in quality between leaf and stem was greatest. Similarly for sheep, Arnold (1960a) found that little selection occurred when young leafy grass swards were grazed, but selection increased as the herbage increased in age and maturity, with green leaf being preferred to mature leaf and stem.

Selection between grass leaf and stem appears to be more extreme on tropical than on temperate swards, but there may be a confounding effect of stage of maturity (Hodgson, 1983). The more rapid and complete lignification of the stem in tropical grasses (Minson, 1981) might have an effect, as might the generally lower leaf to stem ratio and tiller density (Dirven, 1977; Mott, 1983) and the more robust growth form, with coarser tillers and longer and broader laminae (Dirven, 1977). Grazing trials such as those of Chacon and Stobbs (1976) and Hendricksen and Minson (1980) do suggest very strong selection for green leaf by cattle on both tropical grass and tropical legume swards, but the data presented only allow comparisons between diet and mean sward composition, not grazed stratum composition.

L'Huillier et al (1986) compared the proportion of green grass leaf in the diet of grazing sheep with that in the grazed stratum. In three out of four situations there appeared to be strong selection for green leaf, selection increasing as the sward was depleted of this component. Whilst Freer (1981) pointed out that often the preferred plant components are also the most accessible to the animal, L'Huillier et al (1986) found that sheep grazing ryegrass in summer chose to graze largely upon green leaf in the base of the sward rather than on the more accessible but apparently less acceptable dead flowering stem at the sward surface. This suggests that, at least in some circumstances, animal preference assumes a greater importance than considerations of plant component accessibility in determining selection.

To summarise the evidence on the selection of plant components by the grazing animal: in general the preferred component is green leaf, and the degree of selectivity can be strongly influenced by aspects of sward canopy structure. Selectivity normally increases in the following situations: at a higher herbage mass; when the grazed stratum bulk density is lower; when there is a lower proportion of the preferred component in the sward; and when there is a greater contrast in quality between the preferred and less preferred components - for example between leaf and stem in mature swards.

Animal factors affecting selection

Animals exhibit both inter- and intra-specific variation in both preference and selection (Hodgson, 1982a). The intra-specific variation is considered first.

McClymont (1967) stated that selection is the result of innate (instinctive) behaviour plus modifications due to previous grazing experience. According to Arnold and Dudzinski (1978) and Arnold (1981), the animal's physiological state (whether pregnant, lactating or dry) does not appear to affect its dietary preferences, and the effects of breed and age also appear to be small. Hafez and Schein (1962), however, suggested that in cattle the degree of selectivity may be inversely related to the age of the animal; young calves may strip single leaves off stemmy plants whereas adults are more likely to eat whole plants. Zoby and Holmes (1983) found that younger cattle had lower faecal ash and cellulose contents than older cattle grazing the same swards; this suggests that the younger animals grazed more selectively. Variation between individual animals in diet selection may be considerable (Arnold and Dudzinski, 1978; Arnold, 1981).

Moderate fasting of oesophageal fistulated sheep and cattle before they sample a sward generally has little or no effect on the digestibility or chemical composition of the diet (Arnold, McManus, Bush and Ball, 1964; Hodgson, 1969; Chacon and Stobbs, 1977; Sidahmed et al, 1977; Cohen, 1979; Jung and Koong, 1985). Animals fasted as long as 36 hours may be less selective (Sidahmed et al, 1977). However, the between-sheep variation in the chemical composition of extrusa is usually greater than the systematic effects of fasting, experience of a sward and time of sampling on diet selection (Hodgson, 1969).

In many instances, both sheep and cattle select for or against the same components in a sward (Grant and Hodgson, 1980), but it cannot be assumed from this that the two species have the same dietary preferences (Grant et al, 1985). Since the manifestation of preferences as dietary selection is confounded with animal-based limitations, it is difficult to determine whether the preferences of the two animal species are similar, even if they operate in the same sward conditions (Grant et al, 1985).

Cattle are often considered to graze less selectively than sheep (Stobbs, 1975a; Arnold, 1981). Compared with sheep diets from the same sward, cattle diets may contain a higher proportion of dry or dead herbage (Mulholland, Coombe and McManus, 1977; Arnold, 1980) and stem

(Dudzinski and Arnold, 1973; Mulholland et al, 1977; Forbes, 1982a, experiment 3) and have a lower nitrogen and usually higher fibre content (Arnold, 1981).

Hodgson and Grant (1981), Forbes (1982a, experiment 3) and Grant et al (1985) described the results of a series of trials in which sheep and cattle were grazed together on a range of indigenous temperate hill swards. Although patterns of selection between the constitutent species in the plant communities were broadly similar for sheep and cattle, there were several differences in the selective grazing of the two species. Sheep often grazed deeper within the sward canopy and their diets tended to have a higher content of low-growing herbs and a much lower content of flowering stem compared with cattle diets. Sheep were more efficient in maintaining both the proportion of live material in the diet and diet digestibility on poor vegetation, particularly when herbage mass was low. This probably reflected the sheep's greater ability to select from fine-scale mixtures (Grant et al, 1985). Cattle, on the other hand, tended to become progressively less selective than sheep with increasing sward heterogeneity or declining herbage mass (Hodgson and Grant, 1981).

It might be expected that dietary differences between sheep and cattle would be minimal on intensively-managed sown swards compared with tall indigenous swards (Hodgson and Forbes, 1980), and certainly both animal species have been found to graze predominantly in the same (surface) stratum of a sward such as perennial ryegrass (Grant and Hodgson, 1980; Hodgson and Forbes, 1980).

Differences in the selective ability of sheep and cattle may stem from differences in the anatomy of the mouthparts and hence differences in grazing mechanics (Arnold, 1981; Forbes, 1982a). Hodgson (1986) considered that variation in mouthpart structure and size between animal species might have a greater impact on selective grazing than on herbage intake directly. It is generally agreed that a smaller animal species with a small mouth and narrow muzzle has a greater selective ability than a larger species (Bell, 1969; Jarman, 1974; Forbes, 1982a; Owen-Smith, 1982; Short, 1986). Owen-Smith (1982) commented that whereas a narrow muzzle allows the selection of particular clusters of leaves from taller grass swards, a broader muzzle and possibly the use of the tongue in gathering herbage (as in cattle and buffalo) reduce the capacity for selection among tuft components. The broader muzzle is, however, better for maintaining an adequate intake rate from short grass swards (Owen-Smith, 1982) although it may be a disadvantage on very short swards (Clutton-Brock and Harvey, 1983).

The body size of different animal species may determine their feeding strategy (Jarman, 1974; Forbes, 1982a). Smaller animals may have longer searching times and consume a relatively small amount of high quality food, whereas larger animals may accept more abundant food of lower nutritive value (Jarman, 1974). Although the larger-bodied herbivore has a greater absolute food requirement than the smaller animal, it has a lower metabolic rate and can tolerate a lower quality diet (Bell, 1971).

Forbes (1982a) found that when sheep and cattle grazed on the same swards, sheep had a more selective grazing strategy and maintained a relatively constant nutrient concentration in the diet throughout the year. Cattle attempted to maximise their rate of intake rather than maintain a constant nutrient concentration.

<u>The influence of diet selection on ingestive behaviour and herbage intake</u>

In previous sections of this Review, it has been shown that herbage mass and sward canopy structure have a direct effect upon bite weight, rate of intake and consequently herbage intake, by affecting the ease with which herbage is prehended and ingested. In swards in which the process of diet selection is in operation, an additional "layer" of complexity is involved; ingestive behaviour (and hence intake) will also be influenced by the strength of the selection drive and the relative proportions and arrangement of the preferred components within the sward canopy.

Direct evidence on the effects of selective grazing on ingestive behaviour is sparse. Stobbs (1973b) found that bite weight in cows fell as selectivity for leaf increased as swards matured, and selection for leaf has been shown to lead to low bite weights and very low intakes when there is only a small amount of leaf in the pasture (Chacon and Stobbs, 1976; Hendricksen and Minson, 1980). The response in bite rate to increased diet selection may also be to decrease, and for example Seip and Bunnell (1985) found that bite rate in Stone's sheep (a wild sheep species) was significantly reduced when the animals grazed pasture with trace amounts of green herbage in large amounts of dead herbage.

It is easy to understand the decline in bite weight as selectivity increases and presumably fewer plant units are consumed per bite. If these smaller mouthfuls require less chewing before swallowing, the animal should be able to bite at a higher rate, all else being equal. However, if the animal is spending much extra time in searching for and prehending the preferred component, bite rate will presumably decline. Since bite weight generally has a greater influence than bite rate on the rate of intake, it seems likely that whatever the response in bite rate, rate of intake will respond negatively to increasing diet selection. Ultimately, depending on the relative magnitude of the increase in the nutrient concentration of ingested herbage and the decrease in its rate of intake, there may or may not be an advantage to the animal in grazing selectively.

Conclusions

This Review has shown that although a great many experiments have investigated ingestive behaviour in grazing animals and how it is influenced by sward canopy structure, much of the evidence is too general and uncontrolled to allow objective interpretation and meaningful comparison. There is thus a need for critical studies based on recent developments in theory and measurement procedures, and run under controlled conditions. The extremes of control are illustrated by the studies of Black and Kenney (1984) using artificial pastures, and this work (discussed in detail later, with the results of Experiment 2) did give clear-cut answers to some of the important questions. However, trials on artificial pastures cannot substitute for studies on natural swards where the interrelationships between the various sward and animal variables are likely to be more complex and may influence the ranges of sensitivity within a particular relationship. Clearly the influence of sward canopy structure on ingestive behaviour must also be investigated in the "real" grazing situation, on natural swards.

EXPERIMENTAL

Introduction

The Literature Review has indicated that one of the main problems in investigating the independent effects of particular sward variables on the grazing animal's ingestive behaviour and herbage intake is the correlation which normally exists between these variables. Taller swards tend to have a lower bulk density in the surface stratum, and vice versa. Moreover, if the growth period is manipulated in order to produce swards of different height, sward height is likely to be confounded with sward maturity.

A prerequisite of this experimental work was the production of a series of swards with a large and independent variation in sward height and density, whilst minimising differences in sward maturity and digestibility. A range of temperate gramineous forage crops was used, with grasses to provide the shorter swards and cereals to provide the taller swards. For Experiment 1, three swards of contrasting density were produced for each crop by manipulating seed rate at sowing; and most crops were grazed within three months of sowing to minimise differences in digestibility. In Experiment 2, the range of sward conditions was further extended by the use of grazing or cutting pre-treatments.

The two experiments followed contrasting approaches towards identifying the animal's behavioural responses to different sward conditions. In Experiment 1, a series of conventional, large plot grazing trials involved the measurement of herbage intake and the various ingestive behaviour variables as swards were grazed down over several days. Experiment 2 was run under much more controlled conditions which allowed bite weight and its component bite dimensions to be studied in some detail by comparing short-term bite responses between swards. Each approach had its advantages and disadvantages, and the two are compared in the General Discussion.

It should be noted that for each experiment it was necessary to include a certain amount of comment and discussion in the Results section, due to the way in which the set of behavioural response relationships was built up.

In the Discussion of each experiment, the main findings are drawn together and comparisons made with previous work.

EXPERIMENT 1

The influence of sward canopy structure on the ingestive behaviour and herbage intake of grazing animals

Introduction

The series of grazing trials comprising Experiment 1 was run over two grazing seasons, 1983 and 1984. In the first year, the plots were mixed-stocked with sheep and cattle, but in 1984 only sheep were used. All swards were grazed down over a 5-8 day period, and with 3-6 swards grazed concurrently a total of 33 swards were studied over the two years. This design allowed relationships between animal and sward variables to be examined both within and between swards. In addition, it was hoped to compare the responses of sheep and cattle to the same sward conditions in 1983.

In both years, herbage was cut from the experimental crops and frozen for subsequent feeding to sheep indoors. The main objective of the indoor trials was to determine the effect of the internal plant characteristics of each crop on herbage intake, without the limitations that might be imposed by sward canopy structure in the grazing situation.

Materials and Methods

Site and location

The experiment was conducted at the Hartwood Research Station of the Hill Farming Research Organisation which is now part of the Macaulay Land Use Research Institute. The station is situated near Shotts, Lanarkshire (map reference NS 848602).

Seven grazing trials were run each year, between May and October 1983 and between July and October 1984, using gramineous forage crops sown for this purpose. In addition, seven indoor feeding trials were run between June and November 1983, and five during November and

December 1984.

All swards were grown on a gentle south-facing slope at an altitude of approximately 230 m above sea level, on a poorly-drained clay loam of the Rowanhill series. The mean annual rainfall at the station is 1066 mm.

Crops and cropping sequence

The following seven crop species were selected for grazing: rye (Secale cereale), barley (Hordeum vulgare), oats (Avena sativa), perennial ryegrass (Lolium perenne), red fescue (Festuca rubra), timothy (Phleum pratense) and browntop bent (Agrostis tenuis) which is referrred to hereafter as Agrostis. In addition to standard perennial ryegrass cultivars, amenity perennial ryegrass was also used. This was a dwarf cultivar which is normally sown on sports fields or amenity areas, and is referred to hereafter as am. PRG. It was planned to graze the majority of swards as primary growth, but perennial ryegrass was grazed both as primary growth (PRG) and as swards established for one year (PRG1) and four years (PRG4). The crops and cultivars sown are listed in Table E1.1, in the order in which it was planned that they would be grazed in 1983 and 1984.

In planning the cropping sequence, the objective was to graze two contrasting crops concurrently, with no two crops paired together on more than one occasion. Furthermore, the intention was to sow and graze each of the 1983 crops twice during the season. This was not possible in practice as the sowing of the last planned pair of crops (barley and am. PRG) could not be fitted in to the programme. In addition, due to weed infestation problems it was not possible to run a grazing trial on the red fescue sown in June 1983 and because the first pair of crops grazed in 1983 (rye and PRG) was unsatisfactory the results from these two crops are not used in this thesis.

Table E1.1

The crops and cultivars and their sowing dates, listed in the order in which the grazing trials were planned for 1983 and 1984

Year	Planned grazing trial	Crop	Cultivar	Sowing date
1983	I	rye PRG	Rheidol Melle	15 Sept. 1982
	II	barley red fescue	Patty S59	22 April 1983
	III	am. PRG rye	Loretta Rheidol	22 June 1983 8 July 1983
	IV	PRG red fescue	Melle S59	23 June 1983
1984	I	am. PRG oats	Loretta Saladin	24 April 1984 14 May 1984
	II	red fescue timothy	S59 Scots	24 April 1984 11 May 1984
	III	*Agrostis* PRG1	Bardot Melle	11 May 1984 22 April 1983
	IV	barley PRG4	Patty S23	9 July 1984 summer 1980

Table E1.2

The sequence of crops successfully grazed in 1983 and 1984, with details of the timing of measurement periods and the area and stocking of each measurement subplot

Year	Grazing trial	Crop	Measurement period start	Measurement period duration(d)	Number of animals per subplot sheep	Number of animals per subplot cattle	Subplot area(ha) L	Subplot area(ha) M	Subplot area(ha) H
1983	I	barley	28 June	8	4	4 reduced to 2	0.32	0.22	0.14
	II	red fescue	26 July	5	4	2	0.34	0.24	0.18
	III	am. PRG	14 Sept.	6	4	2	0.37	0.19	0.16
		rye	14 Sept.	6	4	2	0.23	0.23	0.19
	IV	PRG	4 Oct.	8	4	3	0.36	0.21	0.19
1984	I	oats	13 July	8	6	0	0.10	0.07	0.07
	II	am. PRG	10 Aug.	8	6	0	0.06	0.05	0.05
		timothy	10 Aug.	8	6	0	0.10	0.07	0.06
	III	*Agrostis*	7 Sept.	8	6	0	0.07	0.15	0.08
		PRG1	7 Sept.	8	4	0	T 0.08		B 0.08
	IV	barley	14 Oct.	8	4	0	0.53		0.12
		PRG4	14 Oct.	8	6	0	S 0.05		Lg 0.02

Consequently, the cropping sequence planned for 1984 did not include repeat sowings of a crop within the year, but rather repeated three of the crops from the previous year, together with three entirely new crops and the two established PRG crops to increase further the range of sward conditions studied.

Only one of the 1984 crops (red fescue) was unsuitable for a grazing trial, and the sequence of crops successfully grazed over the two years is given in Table E1.2. Subsequent comments refer only to these trials, unless stated otherwise.

The young crops and PRG1 were all grown in the same 8.7 ha field; the PRG4 swards were sited approximately 400 m away. Apart from the established PRG, the crops were all sown at three different seed rates, corresponding to 0.5, 1.0 and 2.0 times the recommended commercial seed rate, in order to produce swards with a different herbage mass and density. Table E1.3 indicates the seed rates used for grasses and cereals on the low (L), medium (M) and high (H) sowing density plots, together with the plot areas.

Table E1.3

Seed rates and plot areas for grass and cereal crops

Crop type		Plot L	Plot M	Plot H
			seed rate ($kg\ ha^{-1}$)	
grass		14	28	56
cereal		125	250	500
			area (ha)	
grass or cereal	1983	0.46	0.33	0.24
	1984	0.23	0.16	0.12

The 1983 plots were expected to provide sufficient forage for over ten days' grazing by sheep and cattle; the 1984 plots were half the area of the 1983 plots as they had to support sheep only. The areas of the plots sown at the different seed rates were calculated to allow an approximately similar total mass of herbage on each plot at the start of grazing, assuming the ratio of herbage mass on the low, medium and high plots to be 1:1.5:2.

Alongside the grazing plots, a further 0.15 ha was sown for each crop at the high seed rate to provide forage to cut for the indoor feeding trials. Grazing and cutting plots were sown and managed together.

After preparing a suitable seedbed, each crop was sown with a cereal grain drill. In order to ensure the correct seed rates for the fine-seeded timothy and Agrostis crops, sand was used to dilute the seed and the drill was calibrated accordingly. All crops were sown with the coulters and seed tubes tied up to allow a more even spread of seed over the ground. Cereal plots were then lightly harrowed across the direction of sowing and finally rolled with a Cambridge roller. Grass plots were rolled but not harrowed. Fertiliser was applied to all plots within a few days of sowing, at the rate of 100 kg ha^{-1} of N and 50 kg ha^{-1} of P_2O_5 and of K_2O.

During sward development, all the young crops became infested with weeds, mainly hempnettle (Galeopsis tetrahit) and redshank (Polygonum persicaria) but in some crops also chickweed (Stellaria media) and mayweed (Matricaria spp.). An intensive herbicide application programme was used against the broad-leaved weeds, and in the grass crops sown in 1984 the weeds were so prolific that they had to be topped with a forage harvester and the regrowth sprayed off. Weed grasses such as perennial ryegrass and annual meadow grass (Poa annua) were also present in the swards to varying extents but could not be selectively sprayed out.

The 1984 barley crop required an aphicide application. The oats crop suffered a frit fly attack, causing stunting, and several grass and cereal crops over the two years developed the symptoms of a mildew attack, but these were not treated.

Due to a severe summer drought, the 1984 barley crop had a poor germination and produced exceptionally sparse swards. The adjacent areas sown at the low and medium seed rates for grazing plots, and at the high seed rate for the cutting plot, all produced swards of similar (very low) tiller density. In order to provide sufficient herbage, these swards were fenced and grazed as one unit, the "low" plot, alongside the high seed rate grazing plot which had a noticeably higher tiller density. Consequently, there was no herbage available to cut for an indoor feeding trial.

All other young crops produced three satisfactory grazing plots and one cutting plot, as planned. The two established leys, PRG1 and PRG4, each comprised two swards for grazing, with an additional cutting area for PRG4 only. The PRG1 swards were broadly similar in structure, having received the same mixed (sheep and cattle) grazing pre-treatment and then been allowed a regrowth period of three weeks following fertiliser application at the rate of 68 kg ha^{-1} of N and 15 kg ha^{-1} of P_2O_5 and of K_2O. The two adjacent plots were named "top" (T) and "bottom" (B) according to location in the field, and each was 0.08 ha in area. By contrast, the two PRG4 grazing plots had markedly different sward structures due to different grazing regimes over the preceding grazing season. The 0.05 ha "short" (S) sward had been held under sheep grazing at a constant mean height of 3.0 cm from June to September and was then allowed a four-week regrowth period before the start of the grazing trial. The taller sward which provided the 0.02 ha "long" (Lg) grazing plot and adjacent cutting plot had been used as a holding paddock for sheep during the summer; no detailed records were kept of its pre-trial management.

Animals

Grazing trials

The sheep used in the experiment were Scottish Blackface wethers, one year old at the start of the grazing season. A total of 36 sheep were used in the grazing trials in 1983, and a new batch of 40 sheep in 1984.

The 1983 trials also used 22 Friesian steers which were 12-15 months old at the start of the season. Each plot was stocked with four sheep and 2-4 cattle (depending on the quantity of herbage available) plus an oesophageal fistulate of each species. In 1984, the plots were stocked with sheep only; either four or six non-fistulates plus one fistulated animal.

The oesophageal fistulated sheep and cattle were prepared and subsequently managed largely as described by Rodriguez Capriles (1973). Seven fistulated sheep were used each year, and seven fistulated cattle in 1983. The fistulated sheep originated from the same stock as the non-fistulates; the fistulated cattle were slightly heavier and older than the non-fistulates but of the same breed.

All animals were accustomed to the experimental procedures before the trials started. In the case of the fistulates, only the sheep used in 1983 had been used in a previous experiment, and the other animals were operated on three months prior to the trials to allow time for training to the herbage sampling routine. Identification of individual animals was aided by large eartags on the fistulates, numbered plastic collars of different colours on the non-fistulated cattle, and numbers printed on coloured insulating tape wound round the horns of the non-fistulated sheep.

At the start of the grazing season, the non-fistulated animals were weighed and allocated to six groups, one for each of the maximum of six plots to be grazed at one time (2 crops x 3 density plots). Each group comprised four sheep plus four cattle (1983) or just six sheep (1984), with live weight for each animal species balanced between groups.

A group was assigned to different density plots for different grazing trials, and where possible the same group composition was maintained for the series of crops grazed during the year. However, the full complement of animals in a group was not always required. In addition, before each grazing trial any sheep which was unhealthy or casting deciduous incisor teeth was rejected and a substitute sheep of comparable weight selected.

During each trial, individual fistulates were rotated between plots in an attempt to balance animal effects over plots. The original plan for fistulate allocation had to be modified in 1984 due to difficulty in obtaining extrusa samples from certain animals.

Indoor feeding trials

Four sheep were fed on each crop used in the indoor trials, apart from the 1983 red fescue which only provided sufficient forage for two sheep.

In addition to the six "grazer" groups formed during the initial allocation of sheep in 1983 two groups of four animals were formed for use in the indoor trials only. However, two of these eight sheep had to be replaced before the second and third indoor trials, due to either an unusually low appetite or scouring. The replacement sheep, of similar live weight, had experience from the grazing trials of the crops which they were subsequently fed indoors.

A total of 20 sheep were used in the 1984 indoors trials, with four sheep allocated to each of the five crops such that live weight, as measured in November at the beginning of the series of indoor trials, was balanced over crops. Each animal was used in only one trial and was fed a crop it had previously grazed outside.

General management

Whilst not in use in grazing or indoor feeding trials, all animals were maintained on a short established PRG sward in order to minimise increases in body condition, with corresponding changes in appetite drive, over the season.

Routine health care of the experimental animals is outlined in Appendix 3.

Experimental procedures

Grazing trials

Of the twelve crops successfully grazed over the two years of the experiment, eight crops were grazed in four pairs and four crops were grazed individually (Table E1.2 on p68). For each crop or pair of crops, the different plots were always grazed concurrently.

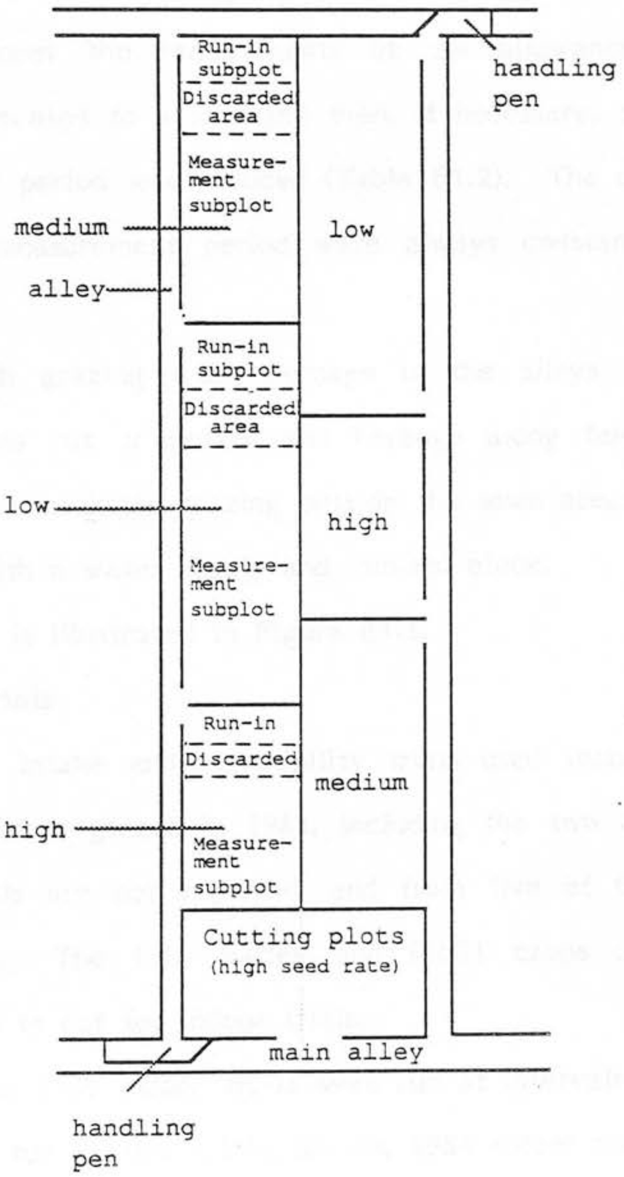
In general, each plot was divided into two subplots, the first ("run-in") subplot being grazed for a two-day acclimatisation period and the second ("measurement") subplot for the eight-day measurement period. Three exceptions were the 1984 PRG1, PRG4 and barley crops, for which the complete plots were required for the measurement period, and the animals were acclimatised on two spare established PRG swards and an oats sward respectively.

All measurements were confined to the measurement subplot. If necessary, its area was reduced before the measurement period in order to give an initial daily herbage allowance of between 36 and 57 g DM kg LW^{-1} for the 1983 barley and red fescue plots, and - after this

Figure E1.1

Plan view (approximately to scale) of the plot layout for a pair of young crops in Experiment 1

Each crop was sown alongside an alley in four adjacent plots; the three grazing plots sown at low, medium and high seed rates and the high seed rate cutting plot. Subdivision of the grazing plots into the run-in subplot and discarded area is also indicated.



allowance was found to be too low - 60 g DM kg LW^{-1} for all other plots. These figures were based on estimates of herbage mass (p78) and measurements of animal live weight made respectively two and four days before grazing started on these subplots. The areas of the measurement subplots are given in Table E1.2.

The allowance was intended to ensure that swards were grazed down to a short stubble over the measurement period and it took no account of concomitant herbage growth. When the crop area was inadequate to meet the requirements of the allowance, first fewer animals were allocated to a plot and then, if necessary, the duration of the measurement period was reduced (Table E1.2). The animal numbers and length of measurement period were always constant across plots within a crop.

Before each grazing trial, herbage in the alleys leading to the handling pens was cut or grazed and herbage along fence lines killed with herbicide, to minimise grazing outside the sown areas. All subplots were provided with a water supply and mineral block.

Plot layout is illustrated in Figure E1.1.

Indoor feeding trials

The indoor intake and digestibility trials used frozen herbage cut from all seven crops grazed in 1983, including the two crops for which the grazing trials are not reported, and from five of the seven crops grazed in 1984. The 1984 barley and PRG1 crops did not provide sufficient forage to cut for indoor trials.

Whereas the 1983 indoor trials were run at intervals throughout the season, between the grazing trials, all the 1984 indoor trials were run in November and December once the grazing programme had finished. Each indoor trial lasted fourteen days, with each crop fed to four sheep, apart from the 1983 red fescue which was fed to only two sheep. Two

Table E1.4

The sequence of crops fed in indoor trials in 1983 and 1984

Year	Start of measurement period	Indoor trial	Crop
1983			
	9 June	1	rye PRG
	18 Aug.	2	barley red fescue
	27 Oct.	3	am. PRG rye
	17 Nov.	4	PRG
1984			
	8 Nov.	1	oats PRG4
	22 Nov.	2	am. PRG timothy
	6 Dec.	3	Agrostis

crops were used per trial, except that in the last trial each year a single crop was fed (Table E1.4.)

Herbage for the trials was cut from the ungrazed cutting plots during one day; usually between days 5 and 7 of the grazing trial measurement period, but up to a week later if persistent rain had kept the crop too wet. Following cutting with a reciprocating mower at a height of approximately 5 cm, the herbage was bagged and stored at -18^{o}C. Before feeding, the taller herbages (all the cereals and timothy) were chopped into lengths of approximately 2.5 cm in a chaff cutter. The shorter crops were not chopped, but each crop was thoroughly mixed before being fed in a partially thawed state.

Throughout each trial, the daily offer was 15% in excess of the previous day's intake on a fresh weight basis. Following a six-day run-in period, the voluntary intake and in vivo digestibility of each crop were estimated for each of two consecutive four-day measurement subperiods. The animals were kept in individual metabolism crates and had constant access to water and mineral blocks. They were subjected to both daylight and, between 08.30 h and 17.00 h, artificial light. Herbage was fed twice daily at 12.00 h and 16.30 h, with refusals collected daily at 09.00 h. During the measurement period, each sheep was harnessed with a canvas faeces collection bag which was emptied each day at 10.00 h.

Grazing trial measurements

The relative timing of the main sward and animal measurements described below is shown for the 1984 grazing trials in Table E1.5.

Sward measurements

Herbage mass. Herbage mass was estimated two days before and over the two days following the end of the measurement period. For the majority of crops, two quadrats (0.15 x 1.22 m) were sited at random in each quarter of a subplot and all rooted herbage cut to ground level

Table E1.5

Experimental timetable for each of the 1984 grazing trials

	Run-in period					Measurement period								Post-grazing		
Day	1	2	3	4	5/0	1	2	3	4	5	6	7	8	1	2	3
		Cr (09.00h) →	→	→	→	→	→	→	→	→	→	→	→			
							FCI	I	II	II	III	III	IV	IV animals off trial		
animals weighed then kept on spare grazing						GT	OF	GT	OF	GT	OF	GT	OF			
						BR		BR		BR		BR				
			MC	F →	→									MC →	→	
					H			H		H		H		H		
				SC →	→				SC					SC →	→	→
				PQ →	→									PQ		
	Cr (15.15h) →	→	→	→	→	→	→	→	→	→	→	→	→			
						FCI	I	II	II	III	III	IV	IV			
		animals onto run-in subplots (17.00h)			animals onto measurement subplots (17.00h)											

BR bite rate recorded manually thrice daily, along with bite depth
Cr Cr_2O_3 dosing (twice daily)
F fences erected to reduce area of measurement subplot
FC faeces collections (four collections in each of four consecutive subperiods; I, II, III and IV)
GT grazing time recorded by vibracorder

H sward height measurements
MC herbage mass cuts
OF oesophageal fistulates sampled for diet digestibility and diet composition estimates
PQ point quadrats
SC stratified clips

Note: All sward measurements were made on the measurement subplots.

with battery-powered clippers. However, only six quadrats per subplot were cut pre-grazing on the PRG1 swards in 1984 and post-grazing on the rye and am. PRG swards in 1983. The PRG4 swards were very dense at ground level and electric shears had to be used to ensure a close cut. The 1984 barley crop was so sparse that quadrat size was increased to 1 m^2 for greater accuracy.

In swards where the crop was growing in drill rows to any extent, the quadrats were aligned at right angles to the rows. Atypically weedy or bare patches were avoided, and if necessary the area of bare ground within a subplot was measured and due allowance made when estimating the amount of herbage present.

Any roots remaining on the cut herbage were removed before it was washed and oven-dried at 90°C for at least twelve hours and then weighed. The mean herbage mass on each subplot was then expressed as kg DM ha^{-1}, and also as kg OM ha^{-1} after duplicate samples of the dried herbage had been milled and ashed at 450°C overnight.

<u>Assessment of sward maturity</u>. Close to each quadrat cut for estimating the pre-grazing herbage mass, an additional small sample of herbage was also cut at ground level. The small clips were bulked per plot and stored at -18°C before being used to assess the maturity of the sward and to estimate tiller density.

First, the clips from a plot were thoroughly mixed and a standard subsampling technique (Grant, 1981) used to select 50 random crop tillers. Visible daughter tillers with more than one leaf were counted as individual tillers and each tiller was classified as either vegetative or reproductive (immature or flowering). In flowering tillers, the flower had either completely or partly emerged, whereas in immature reproductive tillers no flower was visible but nodes were present on the extending stem. The proportion of reproductive tillers was calculated to provide an assessment of the maturity of each sward.

Tiller density. Following the assessment of sward maturity, the 50 tillers were bulked per plot, washed and oven-dried at 90°C for 24 hours. After weighing, the mean dry weight per tiller was calculated for each sward. Next, the point quadrat data (p 84) were used to estimate the proportion of crop material in the sward, and this figure was multiplied by the total herbage mass in order to estimate the herbage mass of crop, excluding weeds. Mean crop tiller density was then calculated as follows:

$$\text{Mean crop tiller density (no. m}^{-2}) = \frac{\text{crop herbage mass (kg DM ha}^{-1})}{\text{mean tiller weight (g DM)}} \times 10^{-1}$$

Sward height. Two measurements of sward height were made: surface height and stem height.

Surface height. The HFRO sward stick (Bircham, 1981; Barthram, 1986) was used to measure the height above ground level of the first contact with the crop; the undisturbed surface height. A total of 40 measurements were recorded per plot.

Stem height. Either the sward stick or a ruler was used to measure the height of the top of the stem on each crop tiller on which surface height had been measured. On an ungrazed vegetative or immature reproductive tiller, this was the height of the ligule of the youngest fully-expanded leaf; on an ungrazed flowering tiller it was the height of the top of the flower; and if the stem had been grazed the height of the severed end was measured.

Both surface height and stem height were measured to the nearest 0.5 cm on rooted vegetation, and no zero readings were taken. Measurements were made in pairs approximately 30 cm apart at random sites, although trampled areas at gateways and watertroughs were avoided.

In 1984, both surface height and stem height were measured at the start and end of grazing and on days 3, 5 and 7 of the measurement period (Table E1.5). In 1983, however, although surface height was measured on each of these five days (or on only the first four days if the measurement period finished early), stem height was measured on only three occasions; before and after grazing and on either day 3 or day 5, depending on the length of the measurement period.

Leaf depth. Mean leaf depth was calculated for each plot from the difference between mean surface height and mean stem height on each day on which both height measurements were taken. Although mean leaf depth was most commonly positive, it could be negative on a hard-grazed crop where mean stem height exceeded mean surface height.

Vertical distribution and bulk density of herbage components and total herbage. These aspects of sward canopy structure were assessed by a combination of two complementary techniques: stratified clips and point quadrats.

Stratified clips. The stratified clip technique generally involved digging turves (approximately 30 x 30 cm) from each plot, transporting them to the laboratory, placing them on their side and harvesting the herbage in successive layers (strata) of equal depth down to the soil surface. The clipped herbage was stored at -18°C before separation into its various components.

In 1983, the area of turf harvested was not measured, but in 1984 a frame was used to delineate an area 23.0 x 23.0 cm (cereal crops) or 15.4 x 15.4 cm (grass crops) within which the layers were cut by battery-powered shears. However, stratified clips for the 1984 timothy and barley swards had to be cut from the standing crop in the field as stable turves could not be dug. In these swards, the frame was set in a horizontal position and moved progressively down the sward as herbage above the frame was cut with hand-operated sheep shears with built-up sides to collect the cut material.

In 1983, five turves were clipped per plot, both pre- and post-grazing. The following year, in addition to six turves clipped pre- and post-grazing, four turves were clipped on day 4 of the measurement period (Table E1.5). Turves were selected to cover the range of heights within the sward and included weed if weed was present. The depth of strata for each crop was selected to ensure that at least five layers were cut per turf, with the minimum depth being 2 cm. The post-grazing clips always used a stratum depth of 2 cm, while pre-grazing depths ranged from 2 to 10 cm between different crops.

A bulked subsample of herbage for separation was taken per stratum per plot per harvest day. Strata cut from cereal crops were separated into the following components: crop green lamina, brown lamina, pseudostem, flowering stem, detached sheath, and flower; weed grass green lamina, brown lamina, pseudostem, flowering stem, detached sheath, and flower; broad-leaved weed green leaf, brown leaf, stem and flower; and brown litter. For the grass crops, the weed grass categories were grouped with the corresponding crop categories to form an "all grasses" set of categories, thus reducing the potential number of categories from seventeen to eleven. Leaf was separated from stem - in gramineous plants the lamina was cut from the stem or sheath at the ligule - and the leaf was classified as green if more than 0.5 of its surface was that colour; otherwise it was "brown". Flowers were severed at the top of the stem.

Each separated fraction from each layer, and the remaining unseparated herbage, was washed, oven-dried at 90°C for 24 hours and then weighed to the nearest 10^{-4}g. The separations indicated the relative proportions by weight of the different herbage components in each layer of the sward. Using the total weight of each stratum and the mean herbage mass for the whole sward (as estimated by mass cuts) the structure of the sward profile was estimated in terms of the density of each herbage component in each stratum, in g DM cm^{-3}.

Point quadrats. The frequency of distribution of the different herbage components within the sward profile was assessed using inclined (32.5°) point quadrats (Warren-Wilson, 1963; Grant, 1981). As the point quadrat needle passed through the sward, the height of each contact was noted to the nearest cm, under the category of crop, weed grass or broad-leaved weed. Contacts were further defined by morphological unit; flower, stem or leaf (i.e. lamina in a gramineous plant) and leaves were classified as green or brown. For each pass of the needle, the height at which the needle reached the ground was also recorded to allow for ground zero correction.

The point quadrat apparatus was sited to cover the range of sward conditions within a plot, but bare patches were avoided. Each time the quadrat was moved to a fresh site (locus), it was aligned in a different direction. In 1983, 70 herbage contacts were recorded per plot before grazing. In 1984, 120 herbage contacts were recorded pre-grazing except on the relatively sparse oats swards on which only 100 contacts were recorded. In addition, 120 herbage contacts were recorded post-grazing on each of the 1984 swards, apart from the sparse timothy and barley swards on which no measurements were taken, and the oats swards on which the required number of contacts was reduced to 70.

The point quadrat data were expressed as the number of contacts per 100 loci per cm of sward height, using the same bands of strata as the stratified clips in order to compare the two techniques.

The use of the data derived from stratified clip and point quadrat measurements is described in the Results section. The key variables obtained were the estimate of the median bulk density of the grazed stratum, and the proportions by weight and bulk densities of the herbage components within that stratum.

Animal measurements

Live weight. The experimental animals were weighed at the start of each grazing trial, four days before they were put onto the measurement subplots. Sheep were weighed to the nearest 0.5 kg, cattle to the nearest 5 kg.

Dentition. At the same time as animals were weighed, their teeth were examined and where possible only animals with sound mouths were selected for the grazing trials. Very few of the cattle shed any deciduous incisors but during each summer the majority of the sheep produced their first pair of permanent incisors.

In August each year, the spread across the incisors (incisor width) of each animal was measured using calipers.

Daily herbage intake. Daily herbage intake was calculated from estimates of daily faecal output and diet digestibility, as described by Le Du and Penning (1982).

Daily faecal output. The chromic oxide (Cr_2O_3) dilution technique was used to estimate mean daily faecal output for each non-fistulated animal on a plot. During each grazing trial, animals were dosed twice daily at 09.00 h and 15.15 h with pellets made from paper impregnated with Cr_2O_3. The sheep pellets weighed 1-2 g and the cattle pellets approximately 5 g and samples of pellets were ashed at 450°C overnight to establish the weight of Cr per pellet, assuming all the ash comprised Cr_2O_3.

Dosing lasted for a total of thirteen days, commencing with a five-day run-in period. Faeces samples were collected from the rectum of each animal twice daily at the time of dosing during the eight-day measurement period, collections starting 24 hours after the animals had been turned onto the measurement subplots. In 1983, faeces samples were bulked per animal into two subperiod collections, each comprising eight individual samples if the crop lasted for the full eight-day measurement period. In 1984, there were four subperiod collections, each comprising four individual samples, as indicated in Table E1.5.

Bulked samples were stored at -18°C until processing. Cattle faeces were thawed for mixing and subsampling and refrozen, and then both sheep and cattle faeces were freeze-dried, milled and mixed and subsamples taken for analysis. Cr content was determined by a modification of the technique described by Williams, David and Iismaa (1962) using atomic absorption spectrophotometry. Faecal ash content was determined by ashing samples at 450°C overnight. The mean daily faecal output for each dosed animal for each subperiod was then estimated as follows:

$$\text{Daily faecal output} = \frac{\text{daily dose of Cr (g)}}{\text{faecal Cr concentration (g gDM}^{-1}\text{)}} \times \left(\begin{matrix}\text{1-faecal ash} \\ \text{proportion}\end{matrix}\right)$$

The mean recovery of Cr using the grab sampling techique was assessed indoors using sheep on a relatively constant level of intake and was found to be 0.996 (s.e. 0.0187) (Appendix 4). This was so close to unity that no correction for recovery was made when calculating faecal output in the grazing situation.

Diet digestibility. The digestibility of the herbage grazed by the non-fistulated animals was estimated from extrusa samples collected from oesophageal fistulates on every alternate day during the measurement period (Table E1.5). The procedure for running the fistulates was as described by Le Du and Penning (1982) and fistulates were run singly rather than in pairs. A foam rubber plug was inserted into the oesophagus below the fistula before sampling in order to improve the recovery of herbage (Appendix 5). After sampling, each fistulate was moved to the plot it was due to sample next in the rotation, two days later. This allowed time for the animal to settle and become accustomed to grazing a new sward.

Extrusa samples were stored at -18°C, then broken up whilst still frozen, mixed and divided into two portions. Two-thirds of each sample was freeze-dried and ground through a 1.0 mm screen to provide subsamples for ash and in vitro organic matter digestibility (IVOMD) analyses. The in vitro procedure was as described by Tilley and Terry (1963), with modifications by Alexander and McGowan (1966), using in vivo standards from forages fed to sheep at 90% of voluntary intake. The remaining third of each sample was used to estimate diet composition.

In order to calculate herbage intake from faecal output and diet digestibility, it was necessary to draw the IVOMD estimates into line with the timing of the subperiods over which the material ultimately forming the faeces would originally have been ingested. A mean rate of throughput of 24 hours was assumed, and hence the intake subperiods were assumed to precede the faecal collection subperiods by this length of time. This meant that in 1984 for example, the intake subperiods lasted from days 0-2, 2-4, 4-6 and 6-8 of the measurement period (commencing in the afternoon and finishing in the morning). The IVOMD was therefore predicted for days 1, 3, 5 and 7 from the measurements taken on days 2, 4, 6 and 8 (Table E1.5). Further details are given in the Results, and the alignment of measurements with the two subperiods in the 1983 trials is outlined on p 93 .

Having determined both mean daily faecal output and the relevant IVOMD value (expressed as a proportion), the mean daily herbage intake was calculated for each non-fistulated animal for each subperiod as follows:

$$\text{Daily herbage intake (g OM)} = \frac{\text{daily faecal output (g OM)}}{1\text{-IVOMD}}$$

In order to aid comparisons, firstly between sheep in the two years of the experiment, and secondly within animals at different ages, daily herbage intake was expressed relative to live weight, as g OM kg LW^{-1}.

Grazing time. Grazing time was measured automatically for non-fistulated animals by Kienzle vibracorder (Allden, 1962; Hodgson, 1982b) with one chart revolution in 24 hours. Charts were changed daily at morning dosing, from 09.00 h. In the first year of the experiment, grazing time was recorded throughout the measurement period, but the continual wearing of vibracorder harnesses caused skin chaffing on both the sheep and the cattle, and often data were lost towards the end of a grazing trial because it was necessary to remove the vibracorders. Consequently, in 1984 grazing time was measured for all animals simultaneously, on alternate days. The vibracorders were put on on the morning of days 1, 3, 5 and 7 and removed after 24 hours.

Although there was usually a vibracorder available for every experimental animal, in 1983 in grazing trial III (am. PRG and rye) only three of the four sheep per plot had a vibracorder. In addition, a few records were lost each year due to failure of the clockwork mechanism, but by covering the join between the two halves of the vibracorder case with a section of car inner tube to stop water from seeping in, the problem was reduced in 1984.

Bite rate. The rate of biting was recorded manually. In general, a bite was characterised both by the sound of herbage being severed and by the upward jerk of the head, but where uprooting of the crop was widespread, such as on the 1984 timothy plots towards the end of the measurement period, individual bites were less distinct. Animals tended to nibble at material lying on the ground, often with no head jerk or sound of herbage being severed, and the observer had to rely on a close view of the animal's head to distinguish prehension and mastication bites.

One observer (the author) collected all bite rate data, using two methods with slightly different definitions of biting activity simultaneously. In method 1, the time taken for 20 bites was recorded by stopwatch, with timing continuing if the animal interrupted its grazing for any reason. However, if the animal was obviously disturbed by the presence of the observer, or if a record lasted for more than two minutes (i.e. the bite rate was less than 10 bites min^{-1}), then the record was abandoned.

Method 2 followed the "20-bite technique" of Jamieson (1975), as modified by Forbes (1982a). The time for 20 bites was recorded on a second watch which was stopped during periods when an animal interrupted grazing by lifting its head to walk or look round the plot, scratch, defecate or urinate. Timing was not interrupted if the animal walked a few paces with the head down nosing the herbage, or lifted its head while chewing herbage in between bouts of biting. If any method 1 record was abandoned, the corresponding method 2 record was also discarded.

In terms of bites per minute, a method 2 observation was equal to or greater than the paired method 1 observation. Method 1 probably gave a closer approximation to the true mean daily bite rate, method 2 indicating a near-maximal bite rate.

Bite rate was measured on all non-fistulated animals thrice daily on every alternate day during the measurement period (Table E1.5). The three 1983 crops with short measurement periods only had three bite rate days but all other crops had four. The exact time of day when the three sets of observations were made varied according to when the animals were grazing, but fell during the period of sunrise to 09.00 h;

between 10.30 h and 15.15 h; and in the evening, before sunset.

Total daily bites. The total number of bites taken by each non-fistulated animal in a day was estimated from the product of grazing time and mean bite rate (method 1) for that day.

Bite weight. The mean weight of herbage ingested per harvesting bite was estimated:

a. directly, for oesophageal fistulated animals;

b. indirectly, for non-fistulated animals.

In the direct method, each extrusa sample collected for IVOMD and diet composition analyses was weighed fresh, and the OM weight calculated following DM and ash determination. This weight was divided by the total number of harvesting bites observed to have been taken by the animal collecting the sample, to derive an estimate of mean bite weight. Such estimates are subject to variability in the recovery of ingested herbage (Appendix 5).

The indirect estimate of mean bite weight for each non-fistulated animal per subperiod was derived from the estimated mean daily herbage intake per subperiod and the appropriate estimate of total daily bites (for the central day of the intake subperiod):

$$\text{Bite weight (mg OM)} = \frac{\text{daily herbage intake (g OM)}}{\text{total daily bites}} \times 10^3$$

Mean bite weight estimated by either method was expressed as mg OM kg LW^{-1}.

Rate of intake. The mean short-term rate of intake of herbage by each non-fistulated animal per subperiod was derived from the estimated mean daily herbage intake per subperiod and the appropriate measurement of grazing time (for the central day of the intake subperiod):

$$\text{Rate of intake (mg OM min}^{-1}) = \frac{\text{daily herbage intake (g OM)}}{\text{grazing time (min)}} \times 10^3$$

As in the case of herbage intake and bite weight, the rate of intake was also expressed relative to live weight - in this case as mg OM kg LW^{-1} min^{-1}.

Bite depth. For each bite rate observation for the non-fistulated animals, a visual assessment was made of the depth below the sward surface to which the animal's head was inserted whilst grazing. This was taken to represent true bite depth (depth of a single bite). The depth of insertion was recorded as falling either within one of five imaginary head depth bands, or approximately along one of the four arbitrary horizontal reference lines marking the limits of the bands. Reference line A passed across the highest visible part of the nostril; B was approximately halfway between A and C; C passed across the base of the eye; and D across the base of the horn for sheep and base of the ear for cattle. A broadly similar system was employed by Forbes (1982a).

The distance from the tip of the muzzle to each of the reference lines was measured for all non-fistulated animals in August each year and mean values were calculated (Table E1.6).

Table E1.6

The distance (cm) from the tip of the muzzle to the four reference lines used to assess the depth of head insertion into the sward, for cattle (1983) and sheep (1983 and 1984)

Reference line	Cattle 1983	Sheep 1983	Sheep 1984
A	4.9	2.4	2.5
B	15.7	8.6	8.9
C	25.6	14.3	14.1
D	40.4	21.0	21.0

It was decided to calculate median rather than mean values for bite depth, since the occasional extreme value would distort the overall mean but not the median. Median values were calculated for each animal species on each plot on each day bite depth was measured. When the median value fell within a head depth band rather than on a reference line, it was considered desirable to assign a single value to the median. The following example is used to illustrate how this was done. If out of a total of fifteen head depth observations obtained for sheep on a particular day in 1984, four fell on reference line A, five in the head depth band between A and B, and six on reference line B, then the median value would be the eighth of these fifteen observations, i.e. the fourth of the five observations in the head depth band. This band, which ranged from 2.5 to 8.9 cm (Table E1.6), would then be subdivided into five equal steps (3.6, 4.6, 5.7, 6.8 and 7.8 cm) and the fourth value, 6.8 cm, assigned to the median.

Bite volume. An estimate of the volume effectively covered by a typical bite in each subperiod was derived from the appropriate estimates of absolute bite weight (indirect method) and the median grazed stratum bulk density:

$$\text{Bite volume (cm}^3\text{)} = \frac{\text{bite weight (mg OM)}}{\text{grazed stratum bulk density (mg OM cm}^{-3}\text{)}}$$

Bite area. The area in a horizontal plane effectively covered by a typical bite in each subperiod was derived from the appropriate estimates of bite volume and the median bite depth:

$$\text{Bite area (cm}^2\text{)} = \frac{\text{bite volume (cm}^3\text{)}}{\text{bite depth (cm)}}$$

Diet composition. The composition of the diet consumed by oesophageal fistulated sheep and cattle was assessed by gross botanical separation of that portion of each extrusa sample which was not required for chemical analyses. Samples for separation were stored at -18°C until required, then thawed and subsampled to provide three equal portions for separation by three observers. Each separation took approximately 30 minutes and the fractions separated by each observer were bulked together within categories corresponding to those used for stratified clip separations. The only difference was that the stratified clip "brown litter" category was replaced by a "roots and unidentified material" extrusa category.

Separated fractions were oven-dried at 90°C for 24 hours and then weighed to the nearest 10^{-4}g. The total dry weight of a separated sample averaged 0.5 g. Diet composition was expressed in terms of the DM proportions of each component.

Diet selection. The degree of diet selection exerted by sheep and by cattle was estimated for each sward on each day the oesophageal fistulates were run, by comparing diet composition with the composition of the grazed stratum. Details of the selection indices used are given in the Results.

Alignment of sward and animal measurements

In order to be able to relate all the sward and animal variables during each measurement period, it was necessary to align all measurements with the timing of the subperiods over which intake was measured. As already mentioned, these intake subperiods were assumed to last from days 0-2, 2-4, 4-6 and 6-8 in 1984, with each subperiod starting in the afternoon and finishing in the morning. The central days in these intake subperiods, days 1, 3, 5 and 7, were selected for the calculation of any intermediate sward or animal measurements not available for these days.

In 1983, when there were only two intake subperiods, these lasted from days 0-4 and 4-8 for the barley and PRG crops (central days; days 2 and 6), from days 0-2 and 2-5 for the red fescue (central days; days 1 and 4), and from days 0-3 and 3-6 for the am. PRG and rye crops (central days; days 2 and 5).

The only exception to this matching up of measurements was for the diet selection data, since relative to the central day in each intake subperiod the extrusa samples were collected one day late during each subperiod in 1984 (on days 2, 4, 6 and 8) and also one day late during subperiod 1 for the 1983 red fescue (on day 2) and subperiod 2 for the 1983 am. PRG and rye (on day 6). As it was not considered feasible to predict diet composition and therefore diet selection for the central intake days from the existing data, diet selection was assessed from sward and diet composition on the extrusa collection days, and this anomaly was left in the data set.

Indoor feeding trial measurements

Herbage offered. Throughout each trial, the level of feeding for each sheep was 15% in excess of the previous day's intake, on a fresh weight basis. During the eight days of the measurement period, while the feeds were being prepared, representative herbage samples were taken in duplicate from each crop for DM estimation. In addition, approximately 1 kg of each crop was taken daily, bulked over the trial and stored at -18°C. A subsample was subsequently freeze-dried, ground through a 1.0 mm screen and analysed for N (by a micro-Kjeldahl method), neutral detergent fibre (NDF) (Van Soest and Wine, 1967) and ash.

Herbage refused. Herbage remaining in the feed bin each morning was weighed fresh, and during the measurement period the DM content was determined daily. Ash content was determined on a sample bulked per sheep per crop over all eight days.

Daily voluntary intake. The daily voluntary intake of each sheep (herbage offered minus herbage refused) was expressed as

g OM kg LW^{-1}. Mean values were calculated per sheep, and hence per crop, for each of the two 4-day subperiods.

Daily faecal output. During the measurement period, the faeces produced by each sheep were collected daily and weighed fresh before being stored at -18^{o}C. The samples were subsequently thawed, bulked per sheep per subperiod and thoroughly mixed before subsamples were taken for DM and ash analyses. Daily faecal output was then expressed on an OM basis.

In vivo digestibility. *In vivo* digestibility (OMD) was calculated from the absolute daily voluntary intake and daily faecal output measured concurrently, as follows:

$$\text{OMD} = \frac{\text{daily voluntary intake (g OM) - daily faecal output (g OM)}}{\text{daily voluntary intake (g OM)}}$$

In vivo digestibility was expressed as a proportion and mean values were calculated per sheep, and hence per crop, for each of the two 4-day subperiods.

Statistical analyses

The statistical analyses for the grazing trials comprised firstly analysis of variance on each of the more important sward and animal variables, and secondly correlation and regression analyses to investigate relationships between these variables.

As will be discussed, very few of the cattle data were analysed statistically. For each of the behaviour and intake variables measured on the 4-6 sheep per plot, apart from bite depth, plot means corrected for any missing values were obtained for each of the two subperiods in 1983 and the four subperiods in 1984. These means were summarised in a three-factor table with no replication of cell entries, and within each year an analysis of variance was run to examine the variation between crops, between plots within crops and between subperiods within crops. The estimate of error was provided by either all (in 1983) or part (in 1984) of the three-factor interaction.

In the case of bite depth, median values were calculated per plot per subperiod directly from the raw data, then subjected to the natural logarithmic transformation and analysis of variance for each year as described above.

The diet selection indices and the majority of the sward measurements were also subjected to analysis of variance within years. The arcsine transformation was used first on the selection indices (which had a potential range of 0 to 1) and on the proportion of leaf in the gramineous fraction of the grazed stratum.

Statistical models were fitted to the raw data on surface height, leaf depth and diet digestibility. These models are described in the appropriate sections of the Results, and as with the other variables three-factor tables were produced.

The three-factor table presented for each variable includes crop means if these were considered important, but the corresponding standard errors are not presented for any variables which were modelled and/or analysed after transformation to the logarithmic scale. Where arcsine transformation was used, levels of significance were calculated on the transformed data but standard errors are quoted from parallel analyses on untransformed data, for reference.

Analyses of variance were also run on the voluntary intake and digestibility data for the four sheep per crop in the indoor feeding trials, in order to examine variation between years and between crops within years. These analyses were followed by correlation and regression analyses to identify variables influencing the voluntary intake of cut herbage. It was anticipated that a covariate term reflecting voluntary intake indoors might be applied to the grazing trial data to remove variation in intake between crops due to crop differences other than structural differences, but as will be explained in the Results such an approach was not found to be appropriate.

After assembling one large data set with the major sward and animal variables from the grazing trials, the key relationships amongst the sward variables, amongst the animal variables, and between the sward and animal variables, were investigated by means of scatter diagrams, correlation matrices and regressions. Biological models of sward variables influencing the key animal responses were built up using multiple regression techniques. Successive x-terms were included if they significantly reduced the residual sum of squares.

All statistical analyses were run on the GENSTAT programme (Lawes Agricultural Trust, copyright 1984), using the facilities of the Edinburgh Regional Computing Centre.

Results

General

The main objective of the experiment, namely to identify responses in herbage intake and ingestive behaviour to different aspects of sward canopy structure, was achieved to some degree for the sheep, although as will be discussed later it did not prove possible to completely isolate and quantify the influence of the different sward variables. Shortcomings in the cattle data precluded a comprehensive investigation of herbage intake and ingestive behaviour responses in this species. There was only sufficient herbage to support two or three steers per plot in 1983, instead of four as originally intended, and consequently only a limited amount of cattle data were collected. In addition, the cattle grazing time data were deficient due to the loss of a high proportion of records, either due to failure of the vibracorder mechanism or because it was necessary to remove vibracorders due to skin chaffing.

Cattle data which were considered to be adequate and were therefore compared with the corresponding data for sheep were: bite depth, diet digestibility and diet selection. All other data presented are for sheep only.

The results given below follow the sequence in which the various measurements were described under Materials and Methods. First, data are presented for each of the individual sward variables and animal responses in the grazing trials, and aspects of diet selection are also considered. Secondly, voluntary intake in the indoor feeding trials is considered in relation to possible causative variables, which might also have to be taken into account in the grazing trials. The final and most important section of the Results then draws together the grazing trial data in an investigation of the interrelationships between the various sward, animal and diet selection variables.

Grazing trials

Sward conditions

The main structural characteristics of each sward prior to grazing are given in Table E1.7, with the crops listed in chronological order. Most crops were grazed at a predominantly vegetative growth stage, and although a few crops had a high proportion of reproductive tillers these were virtually all immature with the flower still enclosed by the stem.

Sward conditions varied widely; tiller density from 300 to 27,400 tillers m^{-2} (ninety-fold) and herbage mass from 300 to 4100 kg OM ha^{-1} (fourteen-fold). There was almost an eight-fold range in the pre-grazing surface height, from 5.7 cm on the 1984 Agrostis M to 44.9 cm on the 1983 barley H.

The 1984 PRG1 herbage mass figures were corrected on the basis of the corresponding values from the statified clips; the original figures were impossible as they indicated that herbage mass was smaller pre-

Table E1.7

Sward maturity, tiller density, herbage mass and surface height prior to grazing

Year and month	Grazing trial	Crop	Plot	Maturity (mean proportion reproductive tillers)	Tiller density (no.m^{-2})	Herbage mass (kgOM ha^{-1}) (n=8) mean	s.e.	Surface height (cm) (n=40) mean	s.e.
1983									
June	I	barley	L	0.77	1380	2470	301	20.4	0.92
			M		2160	2870	262	20.8	1.13
			H		1850	4090	679	44.9	2.08
July	II	red fescue	L	0.00	8890	1340	146	6.4	0.40
			M		6740	1370	143	7.6	0.41
			H		11700	1920	152	12.5	0.76
Sept.	III	am. PRG	L	0.00	5870	1240	129	13.4	0.61
			M		9230	2370	186	15.4	0.68
			H		14120	2880	213	19.5	0.60
Sept.	III	rye	L	0.00	2370	1910	123	18.1	0.57
			M		2400	1880	163	17.8	0.84
			H		3090	2240	160	18.5	0.56
Oct.	IV	PRG	L	0.00	5580	2060	216	18.1	0.64
			M		8500	3540	186	20.5	0.43
			H		9440	3860	175	21.6	0.44
1984									
July	I	oats	L	0.66	560	1500	264	27.0	0.74
			M		1760	2120	317	31.1	1.09
			H		2680	2240	207	28.0	0.85
Aug.	II	am. PRG	L	0.01	7280	2590	133	11.7	0.51
			M		8180	2950	160	14.6	0.65
			H		6480	2900	192	11.1	0.56
Aug.	II	timothy	L	0.33	2620	1620	152	26.4	1.63
			M		4860	2420	412	23.1	1.15
			H		7280	2610	174	31.0	1.44
Sept.	III	Agrostis	L	0.52	13740	2480	277	9.0	0.41
			M		8180	1330	210	5.7	0.43
			H		20690	2030	165	9.9	0.40
Sept.	III	PRG 1	T	0.01	22270	3490[a]	-	11.3	0.66
			B		23660	2560[a]	-	11.6	0.48
Oct.	IV	barley	L	0.28	300	300	64	19.3	1.08
			H		750	1020	51	29.9	1.46
Oct.	IV	PRG 4	S	0.00	27370	1860	154	10.2	0.83
			Lg		22470	3400	225	21.9	3.29

[a] corrected values; see text

Figures E1.2a-e

Photographs of contrasting swards used in the grazing trials

Figure E1.2a

The 1983 barley H, on day 1 of the measurement period
Note that the cattle were grazing the surface stratum of this tall sward.

Figure E1.2b

The 1983 red fescue M, on day 1 of the measurement period
Note the Kienzle vibracorder attached to a head collar worn by the steer to measure grazing time.

Figure E1.2c

The 1984 barley L, on day 3 of the measurement period

Figure E1.2d

The same sward as above, four days later, showing the very low tiller density
Note the Kienzle vibracorder harnessed to the sheep's shoulder.

Figure E1.2e

The 1984 PRG4 Lg, on day 5 of the measurement period

The same sward, ungrazed, can be seen beyond the fence.

grazing than post-grazing.

Photographs of some of the contrasting swards used in the grazing trials are presented in Figures E1.2a-e. Sward conditions during the measurement period are described below.

Herbage mass. Estimated values for the mean herbage mass during each subperiod of the measurement period on each plot are tabulated in Appendix Table E1.1. The data were produced by linear interpolation between the pre- and post-grazing herbage mass estimates, and as expected herbage mass declined over the course of a grazing trial.

Surface height and leaf depth. Mean sward surface height, stem height and leaf depth data were transformed to the natural logarithmic scale and an analysis of variance run on each variable for each year. The transformation was chosen on an empirical basis, and since the leaf depth data included negative values the value of five was added to this data before transformation. Each analysis had two missing values due to the exclusion of two aberrant observations. In addition, in the 1983 data there were nine missing values for surface height and 28 for both stem height and leaf depth, out of a total of 75 values. This was due to the different lengths of measurement period and therefore timing and number of height measurement days in the 1983 trials, and to the reduced frequency of stem compared with surface height measurements in this year.

A full quadratic model, including the deviations term, was fitted to the transformed surface height data for each year, accounting for 0.98 of the variance in each case. Within each year, the differences between crops, between plots within crops, and between days within crops were all highly significant ($P<0.001$). Table E1.8 presents the fitted surface height values for each subperiod on each sward, with intermediate values estimated by linear interpolation on the logarithmic

Table E1.8

The mean surface height (cm) of each sward grazed down over two subperiods (1983) or four subperiods (1984)

Year and month	Grazing trial	Crop	Plot	Subperiod 1	2	3	4	Crop mean
1983								
June	I	barley	L	14.9	8.2			
			M	14.5	8.7			15.4
			H	29.8	16.1			
July	II	red fescue	L	6.0	4.5			
			M	6.2	3.2			5.8
			H	9.6	5.0			
Sept.	III	am. PRG	L	9.8	5.4			
			M	10.9	6.0			8.9
			H	13.6	7.5			
Sept.	III	rye	L	13.1	6.4			
			M	13.3	6.5			9.5
			H	12.1	5.8			
Oct.	IV	PRG	L	13.8	9.4			
			M	14.0	9.4			11.8
			H	14.9	9.4			
1984				1	2	3	4	
July	I	oats	L	20.4	11.8	7.5	4.4	
			M	24.9	15.5	10.6	6.6	13.2
			H	22.8	15.4	11.4	7.7	
Aug.	II	am. PRG	L	10.8	7.5	6.8	4.7	
			M	11.1	7.9	7.4	5.2	7.5
			H	9.6	7.0	6.7	4.8	
Aug.	II	timothy	L	20.2	10.4	5.2	3.9	
			M	15.1	7.6	3.6	2.6	9.4
			H	22.6	11.7	5.8	4.4	
Sept.	III	*Agrostis*	L	8.1	6.6	6.4	5.7	
			M	5.8	4.9	4.9	4.5	6.3
			H	8.2	6.9	7.0	6.5	
Sept.	III	PRG1	T	10.4	9.2	8.6	9.4	9.7
			B	11.0	9.7	9.2	10.1	
Oct.	IV	barley	L	17.2	14.0	7.5	6.3	
			H	26.4	19.8	9.8	7.6	13.6
Oct.	IV	PRG4	S	9.1	6.3	5.5	4.6	
			Lg	16.0	10.0	7.8	6.0	8.2

See text for results of statistical analyses.

scale where necessary. Mean sward surface height usually declined markedly over a grazing trial but there were minor fluctuations on three of the 1984 plots (Agrostis H and PRG1 T and B).

A quadratic model which excluded the deviations term was fitted to the transformed 1984 leaf depth data, accounting for 0.93 of the variance. The full quadratic model was not used as it produced systematic elements of misfit. For the transformed 1983 leaf depth data, a linear model without the deviations term was used since there were only three leaf depth measurements per plot, as compared with five in 1984. The linear model accounted for 0.97 of the variance. Within each year, there were highly significant differences both between crops and between days within crops ($P<0.001$). Plot-within-crop differences were significant only in 1983 ($P<0.05$).

The fitted values for leaf depth over the course of each measurement period, with intermediate values calculated by linear interpolation on the logarithmic scale where necessary, are presented in Table E1.9. Apart from a minor fluctuation on the 1984 PRG4 Lg sward, leaf depth declined as swards were grazed down. A few negative values occurred towards the end of some of the cereal-grazing trials, indicating that the mean stem height exceeded the mean surface height.

A comparison was made between these fitted leaf depth values and the difference between the fitted surface height values described above and fitted stem height values. The model used on stem height was quadratic and included the deviations term in 1984 (five measurements per sward) but was linear and did not include the deviations term in 1983 (three measurement per sward). Regression analysis indicated that the fitted leaf depths were in close agreement with the difference between the fitted surface and stem heights, over the days on which both height measurements were recorded. The

Table E1.9

The mean leaf depth (cm) of each sward grazed down over two subperiods (1983) or four subperiods (1984)

Year and month	Grazing trial	Crop	Plot	Subperiod				Crop mean
				1	2			
1983								
June	I	barley	L	6.0	1.8			
			M	5.8	2.2			4.0
			H	6.8	1.2			
July	II	red fescue	L	3.6	2.7			
			M	4.2	2.5			4.3
			H	7.5	5.3			
Sept.	III	am. PRG	L	6.4	3.4			
			M	7.0	3.6			5.9
			H	9.4	5.6			
Sept.	III	rye	L	2.2	-1.7			
			M	4.7	0.9			0.9
			H	0.9	-1.8			
Oct.	IV	PRG	L	7.4	3.2			
			M	8.2	2.8			4.8
			H	7.3	0.1			
1984				1	2	3	4	
July	I	oats	L	5.2	1.9	0.5	-0.04	
			M	4.6	1.6	0.4	-0.02	1.8
			H	5.2	2.0	0.6	0.2	
Aug.	II	am. PRG	L	6.8	4.0	2.3	1.2	
			M	7.5	4.2	2.1	0.8	3.7
			H	6.7	4.2	2.6	1.5	
Aug.	II	timothy	L	5.1	2.6	1.2	0.4	
			M	3.7	1.9	1.0	0.5	2.2
			H	5.7	2.9	1.3	0.4	
Sept.	III	*Agrostis*	L	3.1	1.8	1.1	0.7	
			M	2.7	1.7	1.2	1.1	2.0
			H	4.1	2.7	1.9	1.6	
Sept.	III	PRG1	T	5.8	5.3	4.8	4.3	5.5
			B	6.8	6.2	5.7	5.2	
Oct.	IV	barley	L	4.4	1.8	0.8	0.5	1.3
			H	3.6	0.8	-0.5	-1.1	
Oct.	IV	PRG4	S	5.9	3.4	2.3	2.0	3.8
			Lg	9.3	4.8	1.3	1.4	

See text for results of statistical analyses.

proportion of variance accounted for was 0.96 and 0.98 in 1983 and 1984 respectively, and whilst the intercept in each regression equation did not differ significantly from zero, the slopes did not differ significantly from one.

Median grazed stratum bulk density. In order to be able to relate animal responses to both sward bulk density and herbage composition in that sector of the sward which was grazed on a particular day, it was necessary first to define the limits of the grazed stratum.

The data on sward canopy structure were investigated with this objective. Attention was focused on the stratified clip rather than the point quadrat measurements. The former had the advantage of being expressed in weight terms in line with the grazing behaviour and diet composition measurements, and the clips were taken more frequently than the point quadrat measurements. Both sets of measurements of the total herbage per stratum or band agreed closely; the correlation between sward bulk density as assessed by the clips and the number of point quadrat contacts per 100 loci per cm at the corresponding height was highly significant ($r^2 = 0.63$, $P<0.001$, $n = 443$ for all data points). The proportion of variance accounted for by the relationship for individual crops ranged from 0.55 ($P<0.001$, $n = 39$) on the 1984 PRG1 to 0.88 ($P<0.001$, $n = 18$) on the 1983 barley.

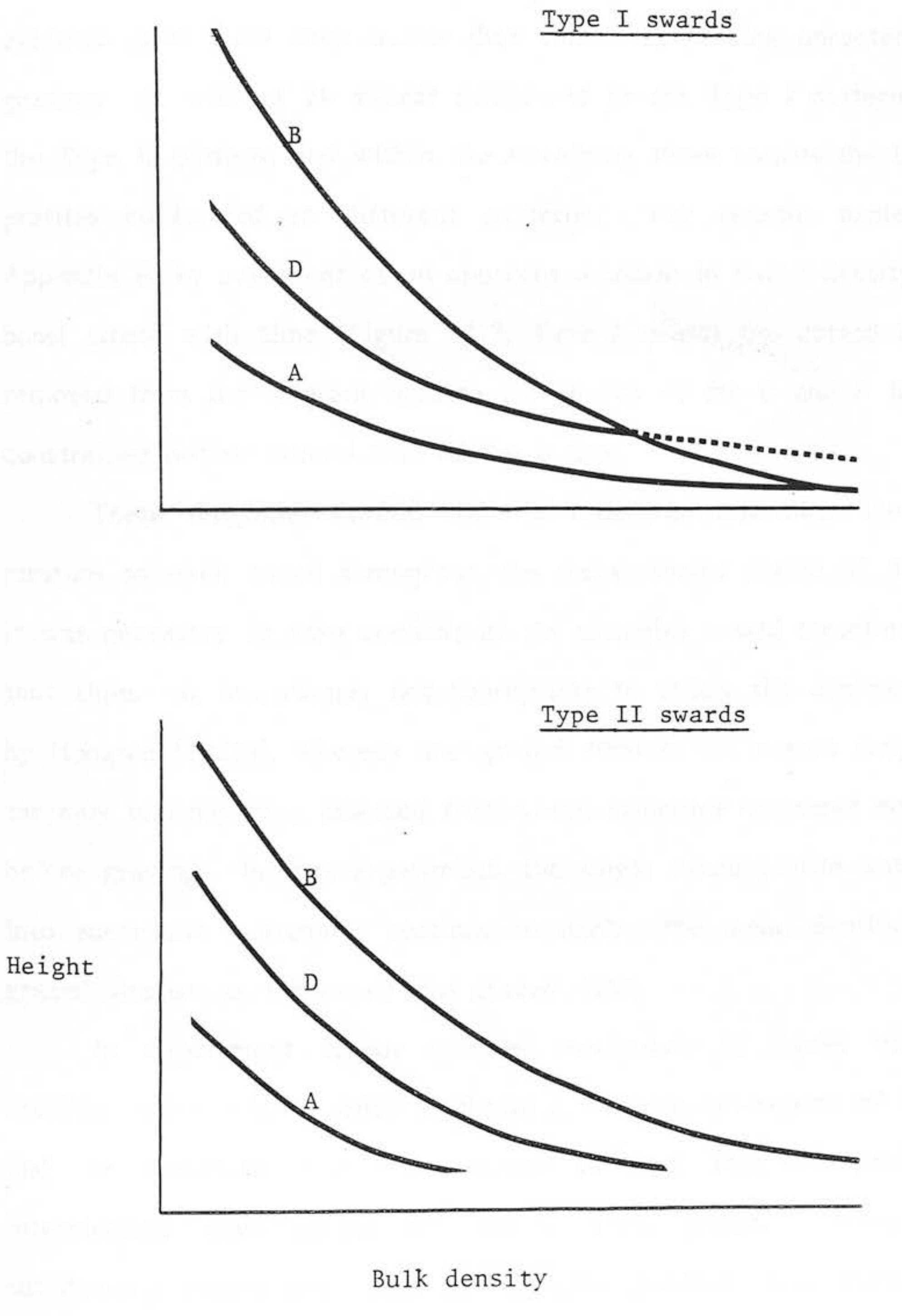
The stratified clip data for the total herbage per stratum were plotted in diagrams illustrating the sward profile. The mid-stratum height (cm) was plotted against the mean density (mg DM cm^{-3}) of that stratum and the resultant points joined by straight lines. By plotting the profiles measured for one sward before (B), after (A), and in 1984 during (D) grazing, changes in sward structure with time could be identified.

Two basic patterns emerged; either the density of the upper part of the profile was reduced whilst that of the lower part remained

Figure E1.3

Typical patterns of change in a sward profile measured before (B), during (D) and after (A) grazing

Type I swards : reduction in density of upper profile; lower profile density unchanged or increased (------)
Type II swards : reduction in density of whole profile



constant or even increased (Type I swards in Figure E1.3; the dotted line denotes an increase in density) or the density of the entire profile was reduced during grazing (Type II swards in Figure E1.3). In the Type I swards, herbage was clearly removed from the upper part of the profile, and it was assumed that the animals were grazing from the sward surface down. The Type II swards were all swards for which there was evidence from field observations that tillers were being uprooted during grazing. A total of 24 swards conformed to the Type I pattern, six to the Type II pattern, and within the remaining three swards the D and A profiles conformed to different patterns. For reasons explained in Appendix 6, in the event of an apparent increase in sward density in the basal strata with time (Figure E1.3, Type I sward) the dotted line was removed from the diagram because the density of the D and A lines was constrained not to exceed that of the B line.

These diagrams showed that in order to determine the grazed stratum on each sward throughout the measurement period of 5-8 days, it was necessary to take account of the changing sward structure during that time. It was clearly not appropriate to follow the approach taken by Hodgson (1981a), whereby the grazed stratum (of swards strip-grazed for only one day) was assessed from sward structure measured only once, before grazing. In that experiment, the single sward profile was divided into successive horizontal sections to derive the mean density of the grazed stratum as the sward was grazed down.

In Experiment 1, an attempt was made to model the sward profiles statistically in order to obtain a succinct description of the lines and to facilitate the interpolation of the relevant profiles on intermediate days during the measurement period. However, no satisfactory model was found in the time available and therefore the intermediate profiles for the 33 swards were interpolated by hand. The set of rules followed to define these profiles is given in Appendix 6, and as an example the profiles interpolated for days 1, 3, 5 and 7 on a Type I sward (1984 oats M) and a Type II sward (1984 timothy M) are illustrated in Figures E1.4a and E1.5a respectively.

As indicated for these same swards in Figures E1.4b and E1.5b, the upper limit of the grazed stratum on a particular day during the measurement period was taken to be the maximum height (y-intercept) on that day. The lower limit of the grazed stratum was either the height of the point of intersection of the profile for that day and the B profile (Figure E1.4b) or occasionally the D profile, or ground level (Figure E1.5b). Thus, in successive measurement subperiods both the upper and lower limits of the grazed stratum generally decreased on a Type I sward (Figure E1.4b), but on a Type II sward the lower limit and occasionally also the upper limit remained constant (Figure E1.5b). Consequently, although the depth of the grazed stratum generally declined with time on a Type I sward (Figure E1.4b), it could decline or remain constant on a Type II sward (Figure E1.5b).

With some overlap between the strata grazed in successive subperiods, as indicated in the two figures, the models of changing sward structure depicted herbage being removed from certain sectors of the sward in more than one subperiod. This was considered to be more representative of the real grazing situation in the current experiment than using a model such as that employed by Hodgson (1981a) in which the sward was assumed to be uniformly defoliated in successive layers.

The model employed in Experiment 1 relied solely upon the stratified clip measurements. The possibility of incorporating the head depth measurements into the model to define the limits of the grazed stratum was investigated as this would remove some of the reliance upon the derived profiles, but this was rejected for several reasons. Firstly,

Figure E1.4

Oats M: a. sward profiles and b. grazed strata, estimated for days 1, 3, 5 and 7 from the profiles measured by stratified clip before (B), during (D) and after (A) grazing

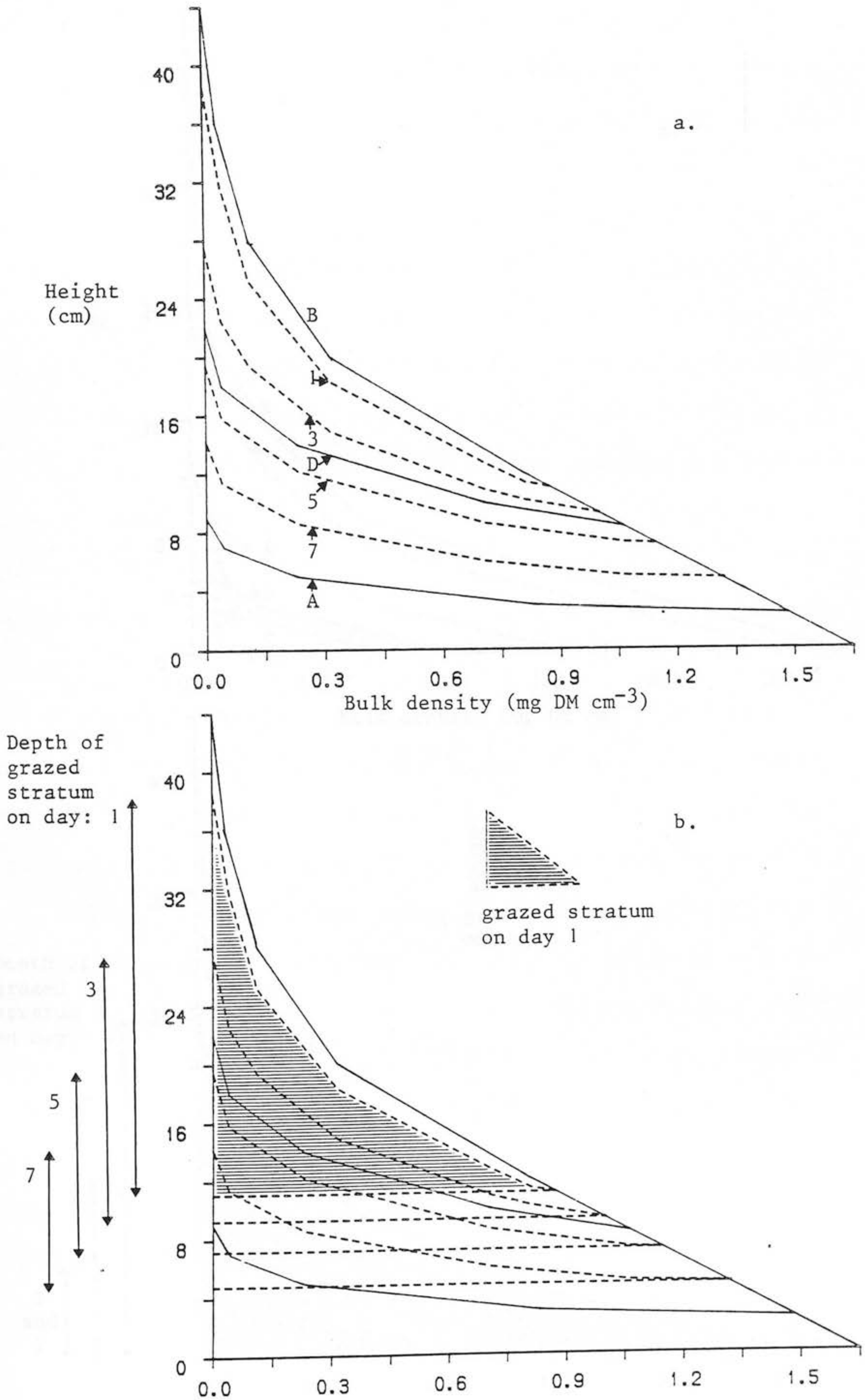
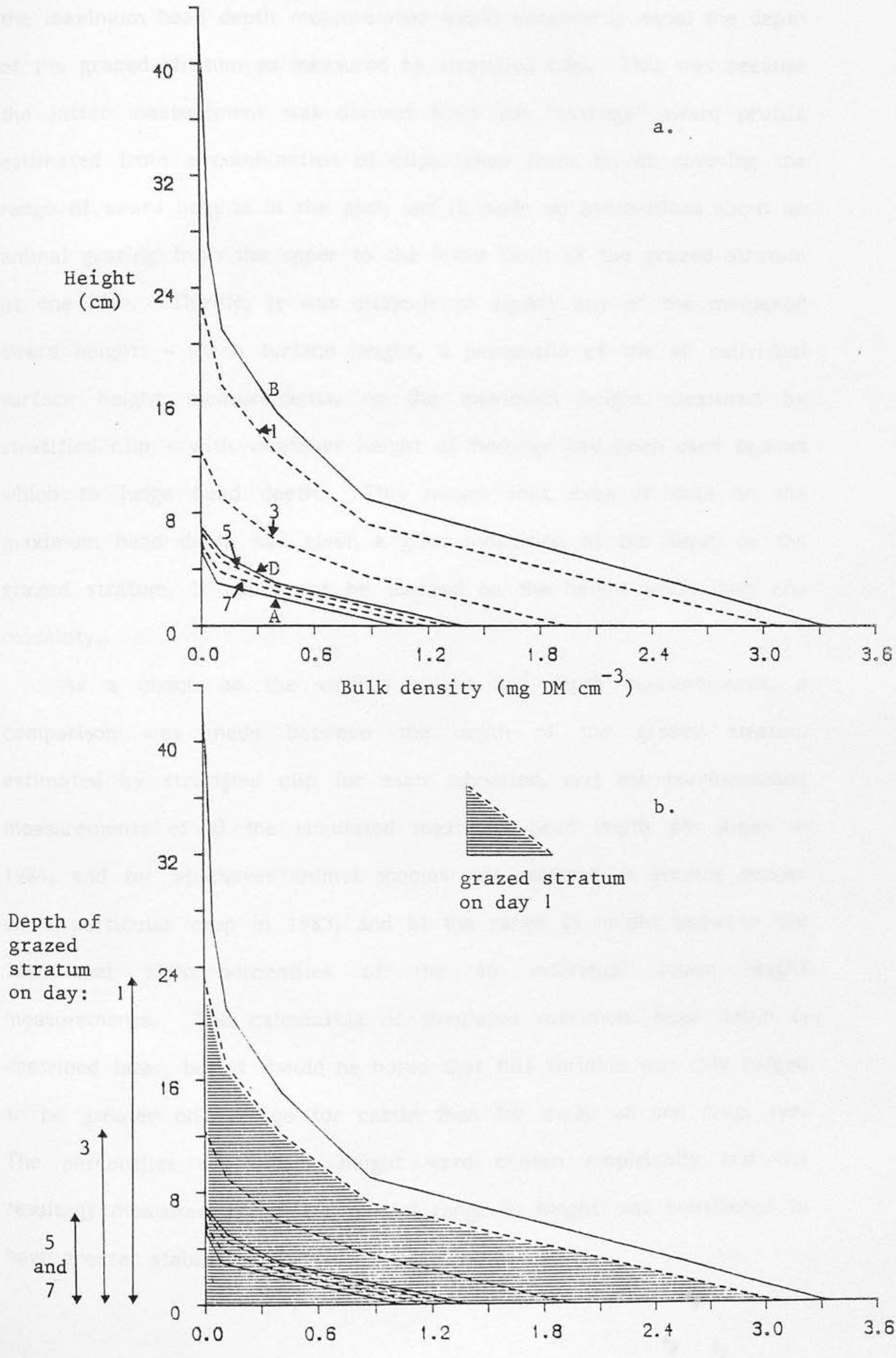


Figure E1.5

Timothy M: a. sward profiles and b. grazed strata, estimated for days 1, 3, 5 and 7 from the profiles measured by stratified clip before (B), during (D) and after (A) grazing



because some of the head depth categories were very broad (over 6 cm), there were shortcomings in the quality of this data. Secondly, not even the maximum head depth measurement would necessarily equal the depth of the grazed stratum as measured by stratified clip. This was because the latter measurement was derived from the "average" sward profile estimated from a combination of clips taken from turves covering the range of sward heights in the plot, and it made no assumptions about an animal grazing from the upper to the lower limit of the grazed stratum at one bite. Thirdly, it was difficult to equate any of the measured sward heights - mean surface height, a percentile of the 40 individual surface height measurements, or the maximum height measured by stratified clip - with whatever height of herbage had been used against which to judge head depth. This meant that even if data on the maximum head depth had given a good indication of the depth of the grazed stratum, it could not be located on the height scale with any certainty.

As a check on the various height and depth measurements, a comparison was made between the depth of the grazed stratum estimated by stratified clip for each subperiod, and the corresponding measurements of a) the simulated maximum head depth for sheep in 1984, and for whichever animal species was assessed as grazing deeper on a particular crop in 1983, and b) the range in height between the 10th and 90th percentiles of the 40 individual sward height measurements. The calculation of simulated maximum head depth is described later, but it should be noted that this variable was only judged to be greater on average for cattle than for sheep on one crop, rye. The percentiles of surface height were chosen empirically and the resultant measurement of the partial range in height was considered to have greater stability than the complete range.

As expected, estimates of the depth of the grazed stratum were greater than the maximum head depths, and they also exceeded the surface height percentile range. However, within each year the positive correlations between the three sets of measurements were highly significant ($P<0.001$), with the r^2 values falling between 0.30 and 0.60 in 1983 ($n = 51$) and between 0.29 and 0.53 in 1984 ($n = 72$). This indicated that despite differences in the absolute values, the depth of the grazed stratum followed a similar trend to the maximum head depth and surface height percentile range, and was therefore considered to be satisfactory.

Consequently, the bulk density of the stratum grazed by sheep on all crops except the 1983 rye was calculated directly from the sward profile diagrams, relying solely on the stratified clip measurements. The median rather than the mean density was obtained, as the former was less sensitive to the shape of the figure representing the stratum grazed on a particular day. The fine detail of the rules followed in interpolating the sward profiles probably had only a minor influence on the median grazed stratum bulk density data.

Using a digitiser plus planimetry software on a microcomputer, the total area of the figure representing the stratum grazed on a particular day was calculated, and then the area of successive horizontal sections of this figure was found until half of the total area lay above, and half below, the horizontal line. At that stage, the length of the horizontal line indicated the median grazed stratum bulk density, which was read off the scale on the x-axis.

For the 1983 rye crop, where the simulated maximum head depth for sheep was on average 0.7 cm less than the corresponding value for cattle, the lower limit of the stratum judged to have been grazed by sheep on a particular day was found by adding 0.7 cm to the lower limit of the grazed stratum identified on the sward profile diagram and assumed to be the stratum grazed by cattle. The median bulk density of this slightly shallower sheep-grazed stratum was then calculated as before.

Finally, since a few random ashings of stratified clip layers on different crops indicated a relatively constant proportion of OM (approximately 0.90), all median grazed stratum bulk densities were converted to OM terms using this figure. The complete set of median grazed stratum bulk density data for sheep is presented in Table E1.10.

Over all plots and subperiods there was a twenty-six-fold range in values, from 0.07 mg OM cm^{-3} on the 1984 barley L, to 1.81 mg OM cm^{-3} on the 1984 PRG1 T. Within a crop, the three plots sown at the low, medium and high seed rates did not always produce swards with densities in the grazed stratum which varied accordingly. In the <u>Agrostis</u> for example, the L plot had the greatest and the M plot the lowest density, but this was clearly due to field conditions. The L plot was situated in the wettest part of the field and was therefore less affected than the H plot, and particularly the M plot, by drought conditions during germination.

Cereals tended to have a lower density than grass swards, and the major source of variation was between crops ($F=8.3$, $P<0.01$ in 1983; $F=317$, $P<0.001$ in 1984) rather than between plots within crops ($F=3.5$, $P<0.05$ in 1983; $F=31$, $P<0.001$ in 1984) or between subperiods within crops ($F=1.1$, n.s. in 1983; $F=10$, $P<0.001$ in 1984). During a trial, the median grazed stratum bulk density tended to increase on a Type I sward, such as the 1984 oats M (Figure E1.4), but on a Type II sward it could either increase, or decrease as in the case of the 1984 timothy M (Figure E1.5). The overall trend between subperiods within a crop was positive except on the 1984 timothy where it was negative.

Table E1.10

The median bulk density (mg OM cm^{-3}) of the stratum grazed by sheep grazing down each sward over two subperiods (1983) or four subperiods (1984)

Year and month	Grazing trial	Crop	Plot	Subperiod 1	2	3	4	Plot mean	Crop mean
1983									
June	I	barley	L	0.47	0.46			0.46	
			M	0.49	0.67			0.58	0.54
			H	0.59	0.59			0.59	
July	II	red fescue	L	1.34	1.03			1.18	
			M	0.60	1.01			0.80	1.00
			H	0.66	1.37			1.02	
Sept.	III	am. PRG	L	0.40	0.49			0.44	
			M	0.86	1.32			1.09	0.82
			H	0.88	0.95			0.92	
Sept.	III	rye	L	0.59	0.57			0.58	
			M	0.45	0.54			0.50	0.62
			H	0.79	0.77			0.78	
Oct.	IV	PRG	L	0.65	0.62			0.64	
			M	1.03	1.17			1.10	1.03
			H	1.28	1.45			1.36	
1984				1	2	3	4		
July	I	oats	L	0.31	0.38	0.47	0.53	0.42	
			M	0.44	0.49	0.55	0.58	0.52	0.49
			H	0.58	0.56	0.52	0.48	0.54	
Aug.	II	am. PRG	L	1.12	1.16	1.21	1.29	1.20	
			M	1.28	1.36	1.34	1.32	1.32	1.32
			H	1.46	1.51	1.47	1.32	1.44	
Aug.	II	timothy	L	0.54	0.70	0.21	0.18	0.41	
			M	1.72	1.10	0.77	0.69	1.07	0.87
			H	1.59	1.21	0.84	0.89	1.13	
Sept.	III	*Agrostis*	L	1.05	1.08	1.41	1.35	1.22	
			M	0.49	0.54	0.65	0.76	0.61	0.92
			H	0.85	0.92	0.95	0.98	0.92	
Sept.	III	PRG1	T	1.64	1.81	1.79	1.66	1.72	1.61
			B	1.38	1.54	1.55	1.53	1.50	
Oct.	IV	barley	L	0.07	0.10	0.13	0.13	0.11	0.15
			H	0.18	0.17	0.18	0.27	0.20	
Oct.	IV	PRG4	S	0.92	1.04	1.16	1.40	1.13	1.20
			Lg	1.08	1.14	1.19	1.65	1.26	

S.e. of plot-within-crop means[a] and significance of differences between plots within crops	1983	0.132*	
	1984	0.042***	
S.e. of crop means[a] and significance of differences between crops	1983		0.076 **
	1984		0.030, 0.027 or 0.024[b] ***

[a] The s.e. presented is an average value; when there are large differences in the size of table entries it may not be appropriate to each entry.

[b] When comparing two crops each with two plots, a crop with two plots with a crop with three plots, and two crops each with three plots, respectively.

<u>Proportions of herbage components within the grazed stratum.</u> The proportions by weight of the main herbage components within the strata grazed by sheep and by cattle were estimated for each day of the measurement period.

The procedure used was as follows. First, the various herbage categories into which the stratified clips had been separated were amalgamated into the following six main categories: gramineous green leaf (lamina), brown leaf, and stem (pseudostem, flowering stem, detached sheath plus flower); and broad-leaved weed green leaf, brown leaf, and stem (including flower). Only very small amounts of brown litter were found in the separations, and on only some crops, and where this component did occur the six main categories were multiplied up to account for the extra weight.

Next, the lower limit of the "grazed" stratum for the sheep in 1984 and the deeper-grazing animal species in 1983 was estimated from the sward profile diagrams for the days on which the B, D and A lines were determined. The lower limit was assumed to be: for the B profile, the point of intersection with the day 1 line; for the D profile, the point of intersection with the B line or ground level; and for the A profile, the point of intersection with the B or D lines or ground level, as appropriate.

For the shallower-grazing species in 1983, the lower limit of each grazed stratum was calculated by adding the mean difference between the simulated maximum head depths for the sheep and cattle on that crop to the lower limit of the stratum grazed by the deeper-grazing species. However, when the grazed stratum ran to ground level for the deeper-grazing species, this was assumed also to be the case for the shallower-grazing species.

In order to calculate the weight of each of the six herbage components within the grazed stratum, the relevant weights for each clipped layer, including the appropriate fraction for the lowest layer which was only partly included in the grazed stratum, were added together. The corresponding weights of each component on the intermediate days were then estimated by linear interpolation between the days on which the clips were taken. Finally, the proportions of the six herbage components within the grazed stratum were calculated from the herbage component weights.

This method of calculating the herbage component proportions avoided any reliance upon the interpolated profiles, except for establishing the lower limit of the "grazed" stratum on the B profile. Since sward composition was interpolated on a complete grazed stratum basis, the density of the various components throughout the sward profile could not be illustrated for the intermediate days, only for the days on which the clips were taken. To illustrate changes in sward composition over the course of a grazing trial, the composition of the 1984 oats M profile before, during and after grazing is shown in Appendix Figure E1.1.

In order to simplify the treatment of the grazed stratum composition data, the herbage categories were further combined to give three simple contrasts: the proportion of gramineous material (as opposed to broad-leaved weed) in the total material; the proportion of green, i.e. live (as opposed to brown, i.e. dead) material in the gramineous fraction; and the proportion of leaf (as opposed to stem) in the gramineous fraction. The second and third contrasts listed above were based only on gramineous material because the proportions of broad-leaved weed were in general relatively low. Within each contrast the two proportions summed to one.

Data for the three sward composition contrasts in the stratum grazed by sheep during each subperiod are presented in Appendix Tables

E1.2, E1.3 and E1.4. Of the three contrasts, both the proportion of gramineous material and the proportion of green material in the gramineous fraction showed only a limited variation (range 0.61 - 1.00 and 0.80 - >0.99 respectively). Indeed, only eight of the 33 plots had less than 0.96 gramineous material (more than 0.04 broad-leaved weed) in the grazed stratum during any subperiod, and in over half the plots there was never less than 0.90 green material in the gramineous fraction of the grazed stratum. The proportion of leaf in the gramineous fraction, however, varied widely; from 0.26 to 0.97. Analysis of variance on this contrast after arcsine transformation indicated significant differences between crops, between plots within crops and between subperiods within crops ($P<0.001$ in each case except for plots within crops in 1983 where $P<0.01$). Between subperiods, the proportions of both leaf and green material in the gramineous fraction tended to decline.

In addition to this sward composition data aligned with the intake subperiods (i.e. data for days 1, 3, 5 and 7 in 1984), data were also obtained for the extrusa collection days (days 2, 4, 6 and 8 in 1984), in order to assess diet selection. Diet selection is discussed at a later stage.

<u>Bulk densities of herbage components within the grazed stratum.</u> The bulk density of the total gramineous material, the gramineous green (live) material and the gramineous leaf within the stratum grazed by sheep during each subperiod were calculated by multiplying the appropriate herbage component proportions by the median grazed stratum bulk density. Data for the three component densities are presented in Appendix Tables E1.5, E1.6 and E1.7.

The range in values in each of these tables was broadly similar to the range in the overall bulk density of the grazed stratum (Table E1.10). As there was comparatively little variation within the proportion of gramineous material or of green material in the gramineous fraction, the bulk densities of these two components tended to follow broadly similar trends to the overall bulk density. Crop, plot-within-crop, and subperiod-within-crop differences reached the same levels of significance. However, whilst both the overall density and the density of gramineous material showed an overall negative trend between successive subperiods on only one crop (the 1984 timothy) the density of gramineous green material showed an overall negative trend on three crops (the 1983 rye and 1984 am. PRG and timothy).

The bulk density of gramineous leaf in the grazed stratum diverged to a greater extent from the overall density than did the other two component densities, but once again the major source of variation was between crops (F=27, P<0.001 in 1983; F=664, P<0.001 in 1984) rather than between plots within crops (F=6.0, P<0.01 in 1983; F=39, P<0.001 in 1984) or between subperiods within crops (F=0.6, n.s. in 1983; F=14, P<0.001 in 1984). The gramineous leaf bulk density showed an overall decrease with time in eight of the twelve crops; the 1983 barley, rye and PRG, and the 1984 oats, am. PRG, timothy, PRG1 and barley.

Animal measurements

Live weight. The live weight records for the non-fistulated animals throughout the grazing season were corrected for differences in gut fill by applying a linear regression with time for each animal individually. From the corrected values, the mean live weight of the sheep on each plot at the start of a trial was found to range from 31.9 to 47.9 kg in 1983, but only from 41.7 to 49.0 kg in 1984 (Appendix Table E1.8). Data on mean cattle live weight are not presented, but ranged from 278 to 363 kg over the fifteen swards grazed in 1983.

Incisor width. The mean incisor widths of the 36 sheep used in 1983, the 40 sheep used in 1984, and the 22 cattle used in 1983 were 3.1 (s.e.

0.03), 3.1 (s.e. 0.02) and 6.3 (s.e. 0.06) cm respectively.

Diet digestibility. Analyses of variance were performed on the *in vitro* organic matter digestibility (IVOMD) data for the extrusa collected from oesphageal fistulated sheep and cattle. Due to samples not being collected, or being discarded because of contamination with rumen contents, three of the 72 values for the 1984 sheep were missing, as were five and three of the 60 values for the 1983 sheep and cattle respectively. In addition, each of the 1983 analyses had nine missing values arising from the shortened measurement period on nine of the fifteen plots.

The three analyses were constrained to allow only linear changes in digestibility with time, and accounted for 0.81 - 0.97 of the variance. In each case, differences between crops and between days within crops were highly significant ($P<0.001$). There were also significant differences between plots within crops for the 1983 sheep ($P<0.001$) and cattle ($P<0.05$) but not for the 1984 sheep.

When a covariate term for the individual animal used to collect a sample on a particular day was included in the analyses, it was significant only for the 1984 sheep ($P<0.05$). Even in this analysis, the covariate gave only a marginal improvement, and since the covariate efficiency was low, leading to large adjustments, it was decided not to include the covariate term in any of the analyses. Consequently, the analyses relied upon the random allocation of animals to plots to disperse any individual animal effects on diet digestibility.

In 1983, the sheep appeared to obtain a diet with a higher IVOMD (mean 0.803) than the cattle (mean 0.778), and a difference in digestibility of 0.02 - 0.03 was maintained across all five crop means. The overall mean IVOMD of the sheep diets in 1984 was 0.797.

Table E1.11

The *in vitro* organic matter digestibility of the diet obtained by oesophageal fistulated sheep grazing down each sward over two subperiods (1983) or four subperiods (1984)

Year and month	Grazing trial	Crop	Plot	Subperiod 1	Subperiod 2	Subperiod 3	Subperiod 4	Crop mean
1983								
June	I	barley	L	0.84	0.84			
			M	0.86	0.84			0.84
			H	0.82	0.82			
July	II	red fescue	L	0.78	0.75			
			M	0.81	0.78			0.78
			H	0.80	0.79			
Sept.	III	am. PRG	L	0.82	0.81			
			M	0.81	0.82			0.81
			H	0.80	0.81			
Sept.	III	rye	L	0.81	0.81			
			M	0.80	0.82			0.81
			H	0.81	0.80			
Oct.	IV	PRG	L	0.81	0.80			
			M	0.81	0.78			0.80
			H	0.80	0.79			
1984								
July	I	oats	L	0.88	0.84	0.80	0.76	
			M	0.82	0.81	0.80	0.78	0.81
			H	0.84	0.83	0.81	0.80	
Aug.	II	am. PRG	L	0.85	0.83	0.82	0.80	
			M	0.84	0.83	0.81	0.80	0.83
			H	0.86	0.85	0.83	0.81	
Aug.	II	timothy	L	0.79	0.78	0.77	0.76	
			M	0.78	0.77	0.76	0.74	0.77
			H	0.77	0.76	0.76	0.75	
Sept.	III	*Agrostis*	L	0.79	0.78	0.76	0.75	
			M	0.81	0.80	0.79	0.79	0.79
			H	0.80	0.80	0.79	0.78	
Sept.	III	PRG1	T	0.81	0.81	0.82	0.82	0.82
			B	0.83	0.83	0.82	0.81	
Oct.	IV	barley	L	0.84	0.83	0.82	0.81	0.82
			H	0.86	0.83	0.80	0.78	
Oct.	IV	PRG4	S	0.79	0.79	0.79	0.78	0.80
			Lg	0.82	0.81	0.80	0.79	

See text for results of statistical analyses.

Table E1.12

The mean daily herbage intake (g OM kg LW^{-1}) of sheep grazing down each sward over two subperiods (1983) or four subperiods (1984)

Year and month	Grazing trial	Crop	Plot	Subperiod 1	2	3	4	Crop mean
1983								
June	I	barley	L	30.3	39.9			
			M	40.0	33.2			36.7
			H	39.0	37.5			
July	II	red fescue	L	38.4	36.0			
			M	54.6	36.4			40.8
			H	39.8	39.6			
Sept.	III	am. PRG	L	38.9	31.6			
			M	34.2	34.3			32.0
			H	27.3	25.4			
Sept.	III	rye	L	40.4	39.3			
			M	30.9	35.4			34.2
			H	30.4	28.8			
Oct.	IV	PRG	L	34.9	24.3			
			M	36.7	18.7			27.3
			H	30.5	18.8			
1984				1	2	3	4	
July	I	oats	L	53.9	36.0	34.0	29.8	
			M	38.6	37.1	32.4	32.5	35.7
			H	41.5	34.5	31.5	27.1	
Aug.	II	am. PRG	L	49.1	41.1	38.6	30.4	
			M	45.4	36.7	31.0	29.8	39.0
			H	53.3	39.4	40.5	32.6	
Aug.	II	timothy	L	33.5	30.9	28.7	32.4	
			M	29.7	26.8	29.6	27.6	28.7
			H	31.7	25.8	23.7	24.0	
Sept.	III	*Agrostis*	L	34.7	30.6	27.2	22.4	
			M	43.7	39.2	33.5	25.9	32.3
			H	38.2	34.4	31.3	26.8	
Sept.	III	PRG1	T	33.5	32.8	25.1	26.2	28.6
			B	34.8	28.0	25.4	23.1	
Oct.	IV	barley	L	29.7	25.1	26.1	21.2	27.1
			H	41.5	31.8	23.8	17.4	
Oct.	IV	PRG4	S	22.6	20.7	14.8	13.1	18.2
			Lg	23.4	21.9	15.0	14.1	
S.e. of crop means and significance of differences between crops				1983				1.86**
				1984				0.72, 0.66 or 0.59[a]***

[a] When comparing two crops each with two plots, a crop with two plots with a crop with three plots, and two crops each with three plots, respectively.

Table E1.13

The mean grazing time (min d^{-1}) of sheep grazing down each sward over two subperiods (1983) or four subperiods (1984)

Year and month	Grazing trial	Crop	Plot	Subperiod 1	2	3	4	Crop mean
1983								
June	I	barley	L	475	659			
			M	519	750			614
			H	572	711			
July	II	red fescue	L	600	794			
			M	631	776			682
			H	583	708			
Sept.	III	am. PRG	L	576	756			
			M	674	800			701
			H	659	743			
Sept.	III	rye	L	532	637			
			M	499	632			602
			H	566	747			
Oct.	IV	PRG	L	672	758			
			M	690	774			714
			H	641	746			
1984				1	2	3	4	
July	I	oats	L	434	588	634	678	
			M	534	665	665	712	628
			H	616	644	612	752	
Aug.	II	am. PRG	L	541	571	682	656	
			M	522	565	644	729	609
			H	506	568	647	674	
Aug.	II	timothy	L	613	764	651	646	
			M	603	671	657	682	662
			H	635	685	662	678	
Sept.	III	*Agrostis*	L	542	709	656	680	
			M	583	740	747	791	684
			H	546	682	762	774	
Sept.	III	PRG1	T	635	672	676	704	628
			B	546	533	660	595	
Oct.	IV	barley	L	530	584	690	699	609
			H	552	666	685	469	
Oct.	IV	PRG4	S	685	680	813	702	652
			Lg	531	638	606	560	
S.e. of crop means and significance of differences between crops				1983				11.0***
				1984				14.7, 13.4 or 12.0[a]**

[a] When comparing two crops each with two plots, a crop with two plots with a crop with three plots, and two crops each with three plots, respectively.

Diet digestibility on the central day of each intake subperiod was estimated for the sheep data by linear interpolation between the corrected digestibility values, and in the case of the first subperiod by extrapolation. The resultant IVOMD values are presented in Table E1.11. The overall range was from 0.74 to 0.88 whilst crop means ranged from 0.77 (1984 timothy) to 0.84 (1983 barley).

Herbage intake. The mean daily herbage intake of sheep on each plot during each subperiod of each trial is shown in Table E1.12. Daily intake varied by a factor of four, from 54.6 g OM kg LW^{-1} in the first subperiod on red fescue M to 13.1 g OM kg LW^{-1} in the last subperiod on PRG4 S. In 1983, intake was significantly different between crops ($P<0.01$) but not between plots within crops, while in 1984 both these sources of variation were highly significant ($P<0.001$). Despite some minor irregularities in the data, the overall trend was for intake on a plot to decline as the sward was grazed down, and subperiods within crops differed significantly ($P<0.05$ in 1983; $P<0.001$ in 1984).

Grazing time. Table E1.13 shows the mean grazing time of sheep on each plot during each subperiod. The range in grazing time was less than two-fold, from 434 to 813 min d^{-1}. Nevertheless there were significant differences between crops ($P<0.001$ in 1983 and $P<0.01$ in 1984), between plots within crops ($P<0.05$ in 1983 and $P<0.01$ in 1984) and between subperiods within crops ($P<0.001$ in both years). The data indicated an overall increase in grazing time over the course of a grazing trial, although in 1984 when there were four subperiods per trial, allowing better definition of the response pattern, there was a tendency in some crops for grazing time to decline towards the end of a trial.

Bite rate. The bite rate data were very similar for the two recording methods with slightly different definitions of biting activity, and since method 1 was preferred as it probably gave a closer estimate of the

Table E1.14

The mean bite rate (bites min^{-1}) of sheep grazing down each sward over two subperiods (1983) or four subperiods (1984)

Year and month	Grazing trial	Crop	Plot	Subperiod 1	Subperiod 2	Subperiod 3	Subperiod 4	Crop mean
1983								
June	I	barley	L	40.6	47.0			
			M	46.2	43.7			41.6
			H	39.2	32.9			
July	II	red fescue	L	49.0	63.6			
			M	42.4	56.2			53.8
			H	47.2	64.4			
Sept.	III	am. PRG	L	57.4	72.0			
			M	50.2	65.8			61.0
			H	56.4	64.0			
Sept.	III	rye	L	46.6	41.6			
			M	44.2	51.7			43.7
			H	37.1	41.1			
Oct.	IV	PRG	L	51.0	59.4			
			M	54.4	54.3			51.2
			H	46.0	42.0			
1984								
July	I	oats	L	43.4	42.5	44.7	35.2	
			M	43.3	45.8	44.5	40.9	42.9
			H	31.2	45.8	50.1	47.2	
Aug.	II	am. PRG	L	38.6	41.3	43.5	49.2	
			M	45.2	47.1	52.2	54.8	48.8
			H	46.4	52.6	58.6	56.7	
Aug.	II	timothy	L	33.5	35.5	36.1	30.6	
			M	36.5	26.8	27.3	29.0	33.6
			H	35.9	40.1	34.5	36.8	
Sept.	III	*Agrostis*	L	55.0	59.8	48.8	48.9	
			M	52.7	58.1	56.7	58.1	53.6
			H	50.3	52.8	49.2	53.4	
Sept.	III	PRG1	T	61.1	55.3	66.2	61.8	61.6
			B	60.6	62.8	57.1	68.2	
Oct.	IV	barley	L	45.0	43.0	43.8	47.1	41.9
			H	37.3	39.6	44.0	35.6	
Oct.	IV	PRG4	S	58.0	65.9	61.0	60.3	51.2
			Lg	48.4	46.3	39.3	30.5	
S.e. of crop means and significance of differences between crops				1983				1.56 ***
				1984				1.22, 1.11 or 0.99[a] ***

[a] When comparing two crops each with two plots, a crop with two plots with a crop with three plots, and two crops each with three plots, respectively.

Table E1.15

The mean number of total daily bites (x 10^2) taken by sheep grazing down each sward over two subperiods (1983) or four subperiods (1984)

Year and month	Grazing trial	Crop	Plot	Subperiod 1	2	3	4	Crop mean
1983								
June	I	barley	L	194	312			
			M	242	329			256
			H	224	235			
July	II	red fescue	L	294	505			
			M	267	433			372
			H	276	456			
Sept.	III	am. PRG	L	336	546			
			M	338	526			432
			H	372	472			
Sept.	III	rye	L	247	267			
			M	222	325			263
			H	211	308			
Oct.	IV	PRG	L	343	451			
			M	373	417			366
			H	295	314			
1984				1	2	3	4	
July	I	oats	L	192	247	282	241	
			M	233	308	298	292	272
			H	208	295	308	356	
Aug.	II	am. PRG	L	212	236	326	327	
			M	239	267	333	399	303
			H	238	301	379	382	
Aug.	II	timothy	L	203	271	232	196	
			M	220	181	181	199	222
			H	229	276	229	249	
Sept.	III	*Agrostis*	L	295	420	318	334	
			M	306	432	426	460	368
			H	278	361	374	415	
Sept.	III	PRG1	T	387	373	452	436	387
			B	330	334	375	406	
Oct.	IV	barley	L	241	250	305	330	257
			H	205	263	293	167	
Oct.	IV	PRG4	S	395	449	498	423	341
			Lg	259	296	237	171	
S.e. of crop means and significance of differences between crops				1983				13.7 ***
				1984				9.5, 8.7 or 7.8[a]***

[a] When comparing two crops each with two plots, a crop with two plots with a crop with three plots, and two crops each with three plots, respectively.

true mean daily bite rate, only this set of data is presented and used in further calculations, e.g. total daily bites.

Overall, the mean bite rate of sheep on each plot during each subperiod ranged almost three-fold, from 26.8 to 72.0 bites min^{-1} (Table E1.14). Bite rate differed between crops ($P<0.001$ in both years), between plots within crops ($P=0.05$ in 1983; $P<0.001$ in 1984) and between subperiods within crops ($P<0.01$ in 1983; $P<0.05$ in 1984). In 1983, bite rate on most plots showed a tendency to increase over the course of a trial, but the bite rate response was less consistent in 1984.

<u>Total daily bites.</u> The mean number of total daily bites estimated to have been taken by the sheep on each plot during each subperiod ranged over three-fold, from 16,700 to 54,600 (Table E1.15). Differences between crops and between subperiods within crops were highly significant in both years ($P<0.001$) whilst plot-within-crop differences were only significant in 1984 ($P<0.001$). The mean number of total daily bites tended to increase as a crop was grazed down, but as with bite rate and grazing time the patterns were less consistent in 1984 than in 1983.

<u>Bite weight.</u> In order to draw a comparison between bite weight estimated directly from extrusa collection, and indirectly by dividing daily herbage intake by total daily bites, both sets of data were expressed on a plot mean basis. This avoided any problems due to missing values in the extrusa data.

The relationship between the two estimates for all 33 plots accounted for only 0.23 of the variance ($P<0.01$) but this was improved to 0.49 ($P<0.001$) when parallel lines were fitted for the two years. The regression equations relating bite weight (mg OM kg LW^{-1}) as estimated from extrusa collection (BWe) to that calculated from intake (BWc), in 1983 and 1984, were:

$$\left.\begin{array}{l} BWe_{1983} = 0.79 \\ BWe_{1984} = 0.29 \end{array}\right\} + 0.72\ BWc\ (\text{s.e. } 0.187)$$

$r^2 = 0.49^{***}$, residual s.d. = 0.37, residual d.f. = 30.

The common slope did not differ significantly from 1, but the intercept in 1983 was significantly greater than 0, indicating that a greater estimate of bite weight was likely to be obtained using oesophageal fistulates than calculating bite weight indirectly. As the intercept in 1984 was not significantly different from 0, there was no significant overall bias to either method in this year.

Although the indirect estimate of bite weight would encompass the accumulated errors inherent in the intake, grazing time and bite rate measurements, these were the preferred data. An accurate assessment of bite weight using the direct method was not always possible, due to problems in counting the bites taken and/or ensuring the throat plug remained in the oesophagus during sampling. In addition, the direct method was based on only a single extrusa collection for each subperiod, whereas the indirect method estimated the mean bite weight of 4-6 sheep.

Consequently, only the indirect estimate of bite weight was considered further. The mean bite weight of non-fistulated sheep on each plot during each subperiod is tabulated in Table E1.16. Values ranged over four-fold in 1983, from 2.02 mg OM kg LW^{-1} in the first subperiod on red fescue M, to 0.45 mg OM kg LW^{-1} in the last subperiod on PRG M. The range was over ten-fold in 1984, from 3.29 mg OM kg LW^{-1} in subperiod 1 on oats L, to 0.31 mg OM kg LW^{-1} on PRG4 S in subperiod 3. The value of 3.29 mg OM kg LW^{-1} was unusually high even for bite weight in the first subperiod; the next highest value was only 2.60 (1984 am. PRG H).

Table E1.16

The mean bite weight (mg OM kg LW^{-1}) of non-fistulated sheep grazing down each sward over two subperiods (1983) or four subperiods (1984)

Year and month	Grazing trial	Crop	Plot	Subperiod 1	2	3	4	Crop mean
1983				1	2			
June	I	barley	L	1.61	1.34			1.52
			M	1.79	1.04			
			H	1.74	1.62			
July	II	red fescue	L	1.36	0.71			1.23
			M	2.02	0.87			
			H	1.53	0.91			
Sept.	III	am. PRG	L	1.23	0.59			0.80
			M	1.06	0.66			
			H	0.74	0.54			
Sept.	III	rye	L	1.64	1.48			1.35
			M	1.44	1.09			
			H	1.45	1.02			
Oct.	IV	PRG	L	1.08	0.56			0.80
			M	1.03	0.45			
			H	1.05	0.60			
1984				1	2	3	4	
July	I	oats	L	3.29	1.49	1.27	1.31	1.49
			M	1.77	1.30	1.12	1.18	
			H	2.06	1.18	1.06	0.84	
Aug.	II	am. PRG	L	2.52	1.81	1.36	1.03	1.50
			M	2.08	1.42	0.94	0.76	
			H	2.60	1.43	1.17	0.93	
Aug.	II	timothy	L	1.73	1.17	1.26	1.74	1.38
			M	1.37	1.55	1.74	1.44	
			H	1.44	0.98	1.09	1.02	
Sept.	III	<u>Agrostis</u>	L	1.20	0.74	0.91	0.72	0.95
			M	1.45	0.99	0.83	0.60	
			H	1.46	0.96	0.85	0.67	
Sept.	III	PRG1	T	0.88	0.92	0.59	0.61	0.77
			B	1.08	0.85	0.68	0.57	
Oct.	IV	barley	L	1.36	1.00	0.93	0.65	1.15
			H	2.06	1.23	0.81	1.14	
Oct.	IV	PRG4	S	0.61	0.48	0.31	0.32	0.63
			Lg	0.97	0.80	0.70	0.88	
S.e. of crop means and significance of differences between crops				1983				0.067***
				1984 0.070, 0.064 or				0.057[a]***

[a] When comparing two crops each with two plots, a crop with two plots with a crop with three plots, and two crops each with three plots, respectively.

Table E1.17

The mean rate of herbage intake (mg OM kg LW^{-1} min^{-1}) of sheep grazing down each sward over two subperiods (1983) or four subperiods (1984)

Year and month	Grazing trial	Crop	Plot	Subperiod 1	2	3	4	Crop mean
1983								
June	I	barley	L	64.4	62.4			
			M	76.9	44.3			61.5
			H	68.1	53.1			
July	II	red fescue	L	63.9	45.3			
			M	87.0	47.0			61.3
			H	68.5	56.0			
Sept.	III	am. PRG	L	67.7	41.6			
			M	50.7	43.0			46.4
			H	41.4	34.3			
Sept.	III	rye	L	76.2	61.3			
			M	62.3	56.5			58.1
			H	53.7	38.9			
Oct.	IV	PRG	L	52.4	32.5			
			M	53.3	24.2			39.2
			H	47.4	25.2			
1984				1	2	3	4	
July	I	oats	L	125.8	62.1	54.4	44.2	
			M	74.0	57.1	48.9	46.4	60.2
			H	67.4	53.6	52.1	36.2	
Aug.	II	am. PRG	L	91.3	71.9	56.3	46.4	
			M	87.9	65.1	48.8	41.2	66.5
			H	108.4	69.4	63.0	48.9	
Aug.	II	timothy	L	54.9	40.7	44.5	50.6	
			M	49.3	40.3	45.7	40.7	43.9
			H	50.3	37.7	36.0	35.6	
Sept.	III	*Agrostis*	L	65.4	43.4	41.9	33.1	
			M	75.3	54.3	45.4	33.0	49.0
			H	69.9	50.5	41.4	35.0	
Sept.	III	PRG1	T	53.0	49.3	37.2	37.1	46.5
			B	65.2	52.5	38.7	39.0	
Oct.	IV	barley	L	57.8	43.1	37.8	30.3	45.8
			H	76.4	47.8	35.4	38.1	
Oct.	IV	PRG4	S	33.1	30.9	18.2	18.7	29.1
			Lg	44.7	35.2	25.0	26.9	

S.e. of crop means and significance of differences between crops:
1983: 3.19**
1984: 2.03, 1.86 or 1.66[a]***

[a] When comparing two crops each with two plots, a crop with two plots with a crop with three plots, and two crops each with three plots, respectively.

Analyses of variance indicated that differences between crops and between subperiods within crops were highly significant in both years ($P<0.001$), whilst plots within crops differed significantly only in 1984 ($P=0.001$). The overall trend was for bite weight to fall, often sharply, during the course of a grazing trial, but in some of the 1984 crops such as timothy the bite weight response patterns were less clear.

Rate of intake. Table E1.17 shows the mean short-term rate of intake of herbage by sheep on each plot during each subperiod. Values ranged almost four-fold in 1983 (24.2 - 87.0 mg OM kg LW^{-1} min^{-1}) but almost seven-fold in 1984 (18.2 - 125.8 mg OM kg LW^{-1} min^{-1}) and the extremes in rate of intake were found on the same plots as the bite weight maxima and minima. Differences between crops and between subperiods within crops were significant in both years ($P<0.01$ in 1983 and $P<0.001$ in 1984) but plot-within-crop differences were only significant in 1984 ($P<0.01$). Responses in rate of intake as a sward was grazed down were broadly similar to responses in bite weight; an overall fall but less distinct patterns in some of the 1984 crops.

Bite depth. The median bite depth of sheep on each plot during each subperiod ranged six-fold from 1.4 to 8.4 cm in 1983, and almost eleven-fold from 1.2 to 13.1 cm in 1984 (Table E1.18). There were four values greater than 10 cm in 1984, all occurring on cereal swards in subperiod 1. Analyses of variance on the median bite depth data transformed to the natural logarithmic scale indicated significant differences between crops ($P<0.01$ in 1983; $P<0.001$ in 1984), between plots within crops ($P<0.05$ in 1983; $P<0.001$ in 1984) and between subperiods within crops ($P<0.01$ in 1983; $P<0.001$ in 1984). The depth of head insertion into the sward generally decreased over the course of a grazing trial, but the pattern was irregular on certain of the 1984 plots.

Table E1.18

The median bite depth (cm) of sheep grazing down each sward over two subperiods (1983) or four subperiods (1984)

Year and month	Grazing trial	Crop	Plot	Subperiod 1	Subperiod 2	Subperiod 3	Subperiod 4	Crop mean
1983								
June	I	barley	L	8.4	2.4			
			M	7.6	2.2			5.9
			H.	8.4	6.5			
July	II	red fescue	L	2.4	2.0			
			M	4.0	1.7			3.4
			H	5.5	4.9			
Sept.	III	am. PRG	L	3.8	1.7			
			M	5.0	4.1			4.0
			H	5.2	4.1			
Sept.	III	rye	L	3.0	1.6			
			M	3.5	2.4			2.4
			H	2.2	1.4			
Oct.	IV	PRG	L	5.2	4.5			
			M	4.4	4.6			4.4
			H	4.0	3.4			
1984				1	2	3	4	
July	I	oats	L	11.5	3.4	1.2	1.2	
			M	13.1	7.0	4.0	2.5	6.0
			H	13.0	5.9	5.7	3.8	
Aug.	II	am. PRG	L	5.7	6.0	6.2	2.5	
			M	6.5	5.7	5.7	5.0	4.7
			H	5.7	2.9	3.2	1.6	
Aug.	II	timothy	L	6.3	4.0	2.5	1.2	
			M	5.1	1.3	1.2	1.2	3.3
			H	6.3	6.7	2.5	1.2	
Sept.	III	*Agrostis*	L	5.3	5.5	5.5	5.3	
			M	4.6	3.4	2.5	1.4	4.6
			H	5.3	5.3	5.5	5.5	
Sept.	III	PRG1	T	5.7	6.0	5.1	5.7	5.3
			B	3.0	5.7	5.7	5.7	
Oct.	IV	barley	L	9.3	6.4	5.4	2.5	6.4
			H	12.5	7.7	5.4	2.2	
Oct.	IV	PRG4	S	5.5	2.5	1.7	1.2	3.0
			Lg	5.5	5.3	1.5	2.5	

See text for results of statistical analyses.

In addition to the median values for bite depth detailed above, maximum values were also required. These were used firstly to assess which sward strata were grazed by the sheep and by the cattle on the mixed-stocked plots in 1983, and secondly for the comparison with the stratified clip estimates of the depth of the grazed stratum (p 114).

As the head depth data were of limited quality due to the comparatively wide recording bands, especially for the cattle (Table E1.6), and as the limited number of observations collected each day on each plot often did not conform to the normal distribution pattern, it was decided to derive a simulated maximum head depth value. This was achieved by adding two standard deviations to the median value on the logarithmic scale, and then back-transforming the derived value. Simulated maxima were in reasonably close agreement with the observed maxima, and correlations between the two were highly significant (r^2 = 0.66 for the 1983 sheep and for the 1983 cattle, r^2 = 0.78 for the 1984 sheep; $P<0.001$ for all three relationships).

A comparison of the head depths of sheep and cattle in 1983 indicated that although the median value appeared to be greater overall for cattle (4.7 cm) than for sheep (4.2 cm), the simulated maximum was, overall, greater for sheep than for cattle (6.8 vs 5.8 cm, s.e. of species mean 0.27 cm, $P<0.01$). The simulated maximum was only greater for cattle on the rye crop, and the mean differences in the simulated maxima for the sheep and cattle on the barley, red fescue, am. PRG, rye and PRG crops were: 1.8, 0.5, 0.0, -0.7 and 3.6 cm respectively.

Bite volume. Data on the estimated volume effectively covered by a bite taken by sheep on each plot during each subperiod are presented in Appendix Table E1.9. The data were very variable, ranging by a factor of eight in 1983 (17 - 144 cm^3) and a factor of 100 in 1984, largely due to the outlying value of 1083 cm^3 for barley L in subperiod 1. Bite volume tended to decline as a sward was grazed down, except on the timothy, and there was a marked contrast in bite volume between crops such as the 1984 barley (mean 436 cm^3) and PRG1 (mean 24 cm^3).

Bite area. Appendix Table E1.10 presents estimates of the area effectively covered by a bite taken by sheep on each plot during each subperiod. Values ranged widely, from 3 to 358 cm^2, and patterns in bite area during the course of a trial tended to be erratic. Bite area did, however, differ between crops such as the 1984 barley (mean 71.8 cm^2) and PRG1 (mean 4.9 cm^2).

Although the data on bite volume and bite area are presented for reference, estimates of both of these bite dimensions were considered to be very crude and need to be treated with a certain degree of caution. A straightforward analysis of variance on either bite dimension was not justified.

Diet selection

Diet selection was assessed by comparing the herbage composition of the extrusa with the corresponding composition of the grazed stratum.

First, the DM proportions of the herbage components in the extrusa samples were combined to give three contrasts for the diet (labelled D) which corresponded with those produced for the grazed stratum of the sward (labelled S). These contrasts were: the proportion of gramineous material (termed "gramineous"), as opposed to broad-leaved weed ("weed"), in the total material; the proportion of green, presumably live, material ("green"), as opposed to brown, presumably dead, material ("brown"), in the gramineous fraction; and the proportion of leaf ("leaf"), as opposed to stem ("stem"), in the gramineous fraction. Within each contrast the two proportions summed to one.

As there were a few missing values in the extrusa data, estimates were obtained for the 1983 sheep, 1983 cattle and 1984 sheep from analyses of variance on the gramineous, gramineous green and gramineous leaf contrasts subjected to arcsine transformation. Since the covariate term for the individual animal used to collect an extrusa sample was significant in only two of the nine analyses, it was decided to exclude it from all analyses of diet composition contrasts, in line with the diet digestibility analyses.

Following the approach taken by Chesson (1978, 1983), selection indices were calculated for each plot on each extrusa collection day, for each of the three contrasts, as follows:

$$\text{Gramineous selection index} = \frac{\dfrac{\text{gramineous D}}{\text{gramineous S}}}{\dfrac{\text{gramineous D}}{\text{gramineous S}} + \dfrac{\text{weed D}}{\text{weed S}}}$$

$$\text{Gramineous green selection index} = \frac{\dfrac{\text{green D}}{\text{green S}}}{\dfrac{\text{green D}}{\text{green S}} + \dfrac{\text{brown D}}{\text{brown S}}}$$

$$\text{Gramineous leaf selection index} = \frac{\dfrac{\text{leaf D}}{\text{leaf S}}}{\dfrac{\text{leaf D}}{\text{leaf S}} + \dfrac{\text{stem D}}{\text{stem S}}}$$

Possible values for each index range from 0 (total rejection of gramineous, gramineous green or gramineous leaf material) through 0.5 (no discrimination between the pair of components in each contrast, such as gramineous and weed material) to 1 (total selection for gramineous, gramineous green or gramineous leaf material).

Since the estimate of diet composition for an animal species on a particular day was reliant upon a single extrusa collection from one oesphageal fistulate, sampling error was potentially high and consequently it was decided that when the diet and sward proportions of a contrast differed by 0.10 or less, the degree of selection for that contrast should be classified as neutral (no discrimination) regardless of the magnitude of the selection index. For diet and sward proportions of a contrast differing by over 0.10, selection was classified as positive when the index fell between the values of 0.5 and 1, and negative when the index fell between 0 and 0.5.

In 1983, both the sheep and cattle diets contained over 0.90 gramineous material, except on the red fescue L where the proportion fell as low as 0.68 for the sheep and 0.23 for the cattle. The proportion of gramineous material in the grazed stratum also reached its lowest value on this plot (0.84 for both sheep and cattle, as compared with a minimum of 0.95 on the other 1983 plots). The animals appeared to be selecting against gramineous material on the red fescue L, the selection index falling with time from 0.30 to 0.12 and from 0.04 to 0.03 for the sheep and cattle respectively. On all other 1983 swards, selection of gramineous material was classified as neutral.

In 1984, the proportion of gramineous material in the sheep diets never fell below 0.88, although the lowest proportion in the sward was 0.57. Consequently, selection for this contrast was either positive (the index ranging from 0.68 to 1.00) or neutral.

The minimum proportions of green material in the gramineous fraction of the sheep and cattle extrusa in 1983 were 0.88 and 0.90 respectively, whilst the minimum proportions in the strata grazed by the two species were 0.76 and 0.74 respectively. The selection response was most commonly classifed as neutral, but positive selection for green material by both sheep and cattle occurred on at least one occasion in five of the fifteen plots. The crops on which this selection occurred were barley, rye and PRG, and the selection index ranged from 0.79 to 0.94 for both animal species.

The sheep diets in 1984 comprised at least 0.82 green material in the gramineous fraction, whilst the swards comprised at least 0.79.

Selection was neutral each day on eleven swards but positive on at least one day on the remaining seven swards. The crops involved were am. PRG, timothy, Agrostis, barley and PRG4, and the index ranged from 0.72 to 0.98.

The proportion of leaf in the gramineous fraction of the diet and of the grazed stratum varied to a greater extent than either of the other two contrasts. In 1983, the proportion in the diet ranged from 0.12 to 0.99 for the sheep and from 0.06 to 1.00 for the cattle; the corresponding proportions in the grazed strata varied from 0.38 to 0.97 and from 0.44 to 1.00. The selection response was consistent within a plot in that it was never positive on one day and negative on another. The sheep showed a consistently neutral response on two plots, a positive response on at least one day on three plots and a negative response on ten plots. The cattle did not appear to discriminate on two plots but responded positively on a further two plots and negatively on eleven. The crops on which the positive responses occurred were am. PRG, and also barley in the case of the sheep, and the index ranged from 0.68 to 0.95 for sheep and from 0.79 to 0.90 for cattle. Negative responses were found within the barley, red fescue, rye and PRG crops, with the index ranging from 0.11 to 0.39 and from 0.01 to 0.38 for sheep and cattle respectively.

In 1984, 0.13 - 1.00 of the gramineous fraction of the diet comprised leaf, while the proportion in the sward ranged from 0.22 to 0.96. Both positive and negative selection responses occurred within six of the plots, a further two plots had consistently neutral responses, and of the remaining ten plots five had neutral or positive responses whilst five had neutral or negative responses. There were no consistent patterns within crops except that the am. PRG and PRG1 apparently never elicited a negative response to gramineous leaf.

In comparing the responses of sheep and cattle to the same swards in 1983, it is interesting to note that although the responses were generally very similar, on average the cattle consumed a marginally lower proportion of gramineous material (0.97 vs 0.98) and leaf material in the gramineous fraction (0.66 vs 0.68) than the sheep. The mean proportion of green material in the gramineous fraction (0.97) was the same for both species.

As an overall indication of the degree of discrimination shown by an animal in grazing each sward, the Kulczynski similarity index (Kulczynski, 1927; Grant et al, 1985) was calculated from the following six proportions in the diet and in the complete grazed stratum: the proportions of gramineous green leaf, brown leaf and stem, and broad-leaved weed green leaf, brown leaf and stem. Since the six proportions within the diet or sward always summed to one, the Kulczynski index was calculated simply by adding the lower figure from either the diet or sward for each of the six proportions. An index of 0 would indicate complete dissimilarity between the diet and grazed stratum (and therefore could not occur in this experiment) whilst the maximum value of 1 would indicate complete similarity, the animal consuming the six herbage components in exactly the same proportions as they occurred in the grazed stratum.

Table E1.19 presents the Kulczynski similarity index for sheep on each plot during each subperiod - usually one day late relative to the timing of the other measurements, as explained previously. Overall, the index ranged from 0.32 to 0.97. A total of six values missing in the original data were estimated from analyses of variance for each year after the data had been subjected to arcsine transformation. The analyses indicated significant differences in 1984 between crops ($P<0.001$), between plots within crops ($P=0.001$) and between subperiods

Table E1.19

The Kulczynski index of similarity between the diet composition and the composition of the stratum grazed by sheep grazing down each sward over two subperiods (1983) or four subperiods (1984)

Year and month	Grazing trial	Crop	Plot	Subperiod 1	2	3	4	Crop mean
1983								
June	I	barley	L	0.86	0.82			
			M	0.88	0.59			0.74
			H	0.70	0.60			
July	II	red fescue	L	0.79a	0.77			
			M	0.83	0.74			0.83
			H	0.95a	0.90			
Sept.	III	am. PRG	L	0.95	0.93			
			M	0.86	0.71			0.86
			H	0.96	0.76			
Sept.	III	rye	L	0.69a	0.84			
			M	0.89	0.91			0.82
			H	0.88	0.71			
Oct.	IV	PRG	L	0.92	0.95			
			M	0.90	0.94			0.88
			H	0.88	0.68			
1984				1	2	3	4	
July	I	oats	L	0.57	0.60	0.68	0.70	
			M	0.90	0.88	0.94	0.93	0.76
			H	0.51	0.88	0.80	0.69	
Aug.	II	am. PRG	L	0.53	0.32	0.33	0.57	
			M	0.75	0.46	0.48a	0.41	0.54
			H	0.68a	0.69	0.62	0.67	
Aug.	II	timothy	L	0.85	0.66	0.56	0.52	
			M	0.86	0.87	0.82	0.76	0.77
			H	0.89	0.86	0.66	0.88	
Sept.	III	*Agrostis*	L	0.70	0.74	0.79	0.87	
			M	0.45	0.94	0.80	0.93	0.79
			H	0.84	0.85	0.77	0.78	
Sept.	III	PRG1	T	0.97a	0.96	0.89	0.89	0.92
			B	0.96	0.93	0.89	0.85	
Oct.	IV	barley	L	0.89	0.90	0.83	0.78	0.85
			H	0.78	0.87	0.83	0.94	
Oct.	IV	PRG4	S	0.79	0.76	0.60	0.52	0.73
			Lg	0.92	0.92	0.81	0.54	

S.e. of crop means and significance of differences between crops: 1983 0.034 ns.; 1984 0.030, 0.028 or 0.025[b] ***

[a] estimated value

[b] When comparing two crops each with two plots, a crop with two plots with a crop with three plots, and two crops each with three plots, respectively.

within crops (P<0.05), but in 1983 the first two sources of variation were significant only at the 0.10 probability level and differences between subperiods within crops were not significant. Nevertheless, there was a tendency for the similarity index on the majority of plots in 1983 to decrease during the course of a grazing trial, indicating that animals tended to become increasingly selective when grazing the lower sward stata. In 1984, trends in the index varied considerably between plots, although there was an overall decline, indicating increasing diet selection, as four of the seven crops were grazed down.

A comparison of the similarity indices for sheep and for cattle in 1983 indicated that overall the cattle tended to be slightly more selective. Individual values ranged from 0.59 to 0.96 (mean 0.83) for the sheep, compared with 0.26 - 0.98 (mean 0.78) for the cattle. In general, the crop mean values for the cattle and for the sheep differed by less than 0.05, but on the red fescue the crop mean index was 0.63 for the cattle compared with 0.83 for the sheep. Within a plot, cattle generally appeared to become increasingly selective with time, like the sheep.

Indoor feeding trials

An examination of the crop mean values for both daily voluntary intake and *in vivo* organic matter digestibility (OMD) in the indoor feeding trials indicated that the data were more stable in the second subperiod than in the first. Therefore, data are presented for the second subperiod only, except in the case of the 1983 red fescue. Since this crop was fed to two instead of four sheep, the data for both subperiods were used in place of data for four individual sheep.

Daily voluntary intake. The mean daily voluntary intake on the seven crops fed in 1983 ranged from 15.5 to 37.2 g OM kg LW^{-1}, whilst the range over the five crops fed in 1984 was only from 13.4 to 18.6 g OM kg LW^{-1} (Table E1.20). Differences between years, and between

Table E1.20

The mean daily voluntary intake of sheep, in vivo organic matter digestibility and daylength during the indoor feeding trials in 1983 and 1984

Year and month	Trial	Crop	Daily voluntary intake (g OM kg LW^{-1})	In vivo organic matter digestibility	Daylength (h daylight d^{-1})
1983					
June	1	rye	31.6	0.72	17.53
		PRG	37.2	0.81	
Aug.	2	barley	34.8	0.82	14.53
		red fescue	30.2	0.72	
Oct.	3	am. PRG	24.7	0.80	9.23
		rye	22.7	0.79	
Nov.	4	PRG	15.5	0.81	7.88
mean			28.1	0.78	12.92
1984					
Nov.	1	oats	18.3	0.78	8.38
		PRG4	14.4	0.81	
Nov.	2	am. PRG	17.5	0.77	7.58
		timothy	18.6	0.69	
Dec.	3	Agrostis	13.4	0.74	7.08
mean			16.4	0.76	7.80
s.e. of means per year			0.70	0.004	
s.e. of crop-within-year means			1.68	0.011	
significance of differences					
between years			***	***	
between crops within years			***	***	

crops within years, were highly significant ($P<0.001$).

In vivo digestibility. The OMD of the crops ranged from 0.72 to 0.82 in 1983 and from 0.69 to 0.81 in 1984 (Table E1.20). As in the case of voluntary intake, there were significant differences in OMD between years and between crops within years ($P<0.001$).

Crop composition. The DM content of the twelve crops ranged from 0.13 to 0.31, and within the DM fraction the OM content ranged from 0.82 to 0.95, the N content from 0.016 to 0.043 and the NDF content from 0.33 to 0.53.

Relationships between daily voluntary intake and crop characteristics and daylength

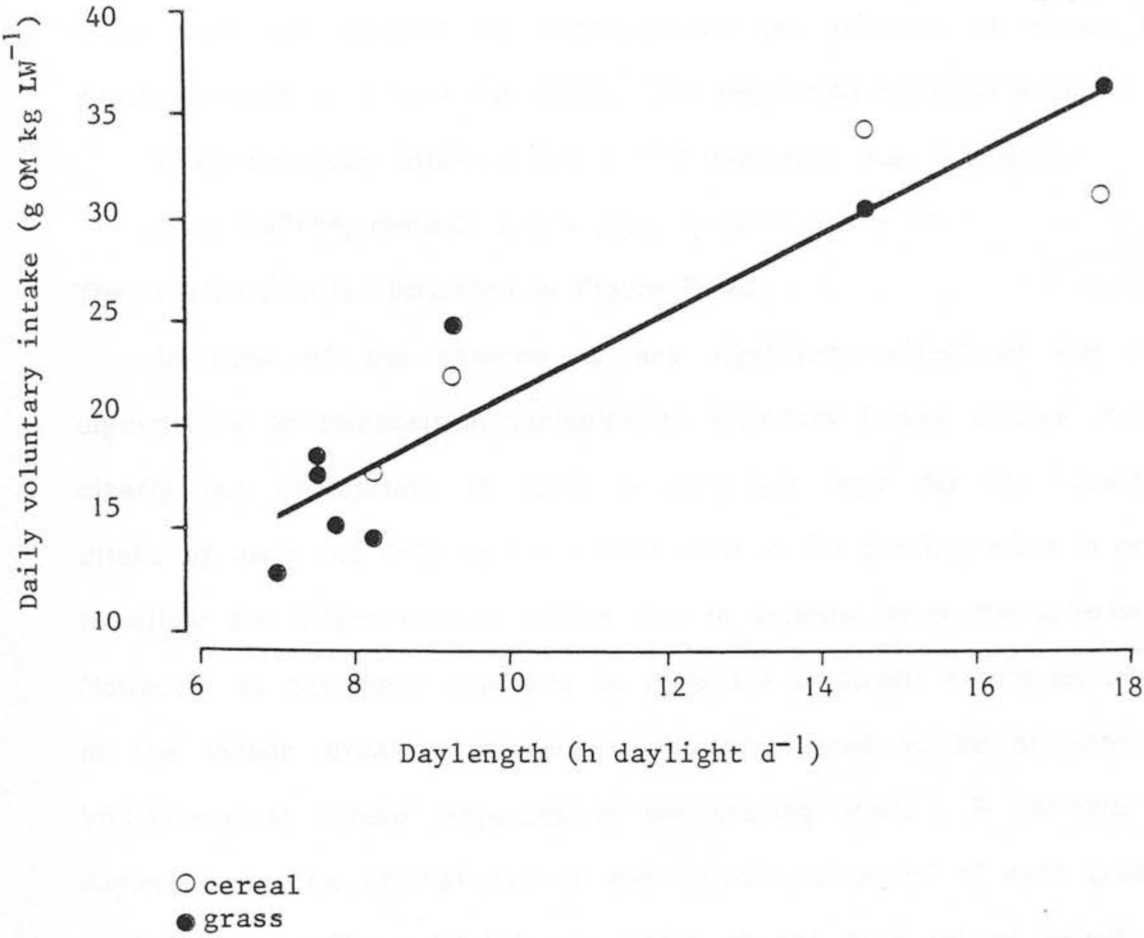
As a seasonal trend in daily voluntary intake was apparent from the data, a variable for the number of hours of daylight on the second day of the second measurement subperiod of each indoor trial was included with the crop variables under consideration as having a potential influence on voluntary intake. Daylength ranged from 7.08 to 17.53 h daylight d^{-1} (Table E1.20) and although crops were fed throughout the season in 1983, in 1984 all the crops were fed towards the end of the year when daylength was short.

It was recognised that variables with a seasonal pattern other than daylength might have influenced intake. Animal age was considered unlikely, although the level of body fat was a possibility. The sheep appeared to gain in condition during the summer of 1983, but it is doubtful whether they became so obese by November that their intake was halved. Unfortunately, no records were kept of body condition score during either the indoor feeding trials or grazing trials.

Scatter diagrams, a correlation matrix and regression analyses were used to investigate the relationships between daily voluntary intake and the OMD of the crops, their DM, OM, N and NDF contents, and

Figure E1.6

The relationship between the daily voluntary intake of sheep and daylength in the indoor feeding trials



daylength. Surprisingly, intake was not significantly related to crop digestibility ($r^2 < 0.01$) or any of the measures of crop composition ($r^2 \leqslant 0.21$).

By far the strongest relationship was with daylength. There was a simple linear relationship between daily voluntary intake and daylength which was not significantly improved by the addition of either the quadratic term or a term for OMD. The regression equation was:

Daily voluntary intake = 2.4 + 1.93 daylength (s.e. 0.235);

r^2 = 0.87***, residual s.d. = 3.14, residual d.f. = 10.

The relationship is illustrated in Figure E1.6.

In view of the absence of any significant effect of the crop digestibility or composition variables on voluntary intake indoors, it was clearly not appropriate to apply a covariate term for the voluntary intake of each cut crop to the intake data in the grazing trials in order to allow for differences in intake due to internal crop characteristics. However, as daylength appeared to have the dominant effect on intake in the indoor situation, daylength was considered to be of potential importance to intake responses in the grazing trials. A variable for daylength on the central day of each intake subperiod of each grazing trial (Appendix Table E1.11) was added to the data set of sward and animal variables measured in the grazing trials. Over the two years daylength ranged from 10.0 to 17.5 h daylight d^{-1}.

The interrelationships between sward variables, ingestive behaviour, diet selection and herbage intake

The interrelationships between the various sward and animal variables measured in the grazing trials were examined initially by means of correlation matrices and scatter diagrams. Only data collected for the sheep, not the cattle, were included, and the animal variables were: herbage intake, grazing time, bite rate, total daily bites, bite weight, rate of intake, median bite depth, bite volume, bite area and the Kulczynski similarity index. Diet digestibility was treated as a sward variable, along with herbage mass, surface height, leaf depth, the median grazed stratum bulk density, the proportions and bulk densities within the grazed stratum of gramineous material and of green material and leaf within the gramineous fraction, and tiller density (the last variable for subperiod 1 data only). A variable was also included for daylength in each subperiod.

Attention was focused on the following two data sets:

a. the complete data set, using the measurements from each of the two subperiods in 1983 plus those from the four subperiods in 1984 (n = 102);

b. the data from subperiod 1 in each year (n = 33).

Thus, relationships for the complete data set encompassed both a within- and a between-sward component, whilst relationships for the subperiod 1 data were based on a comparison between swards only. The first subperiod was used in order to minimise any confounding of true between-sward effects with the effects of stage of defoliation, fouling and trampling.

Correlation matrices, together with data summaries for each variable, are given in Appendix 7 for data sets a. and b. These matrices, along with scatter diagrams and regression analyses, were used to investigate the relationships between:

1. the various sward characteristics;
2. herbage intake, ingestive behaviour and diet selection;
3. the key behaviour and sward variables.

Interrelationships between sward variables

As expected, herbage mass and sward surface height were positively related, as were herbage mass and the grazed stratum bulk density (Appendix 7). The negative relationship between surface height and grazed stratum bulk density was significant over the complete data set ($r^2 = 0.05$, $P<0.05$), and although it was not significant for the subperiod 1 data due to the reduced number of degrees of freedom, there was evidently still a weak association ($r^2 = 0.09$). Moreover, in the latter data set surface height was also negatively related to the bulk density of gramineous leaf in the grazed stratum ($r^2 = 0.18$, $P<0.05$). Clearly a rigorous separation of sward height and density was not achieved, even in the subperiod 1 data set based on a between-sward comparison.

Additional confounding of variables was also evident. There was a negative relationship between surface height and the proportion of leaf in the gramineous fraction of the grazed stratum in the subperiod 1 data ($r^2 = 0.39$, $P<0.001$). Surface height was positively related to diet digestibility in the complete data set ($r^2 = 0.24$, $P<0.001$) although the two variables were better dissociated in subperiod 1 ($r^2 = 0.08$, n.s.). Conversely, diet digestibility was significantly negatively related to grazed stratum bulk density in subperiod 1 ($r^2 = 0.15$, $P<0.05$) but not over all data ($r^2 = 0.02$).

Interrelationships between herbage intake, ingestive behaviour and diet selection

Appendix 7 shows that the relationships between herbage intake and the various ingestive behaviour variables were very similar for both the complete data set and subperiod 1 data. By far the strongest (positive) relationships with herbage intake were those involving the short-term rate of intake or bite weight (r^2 ranging from 0.59 to 0.84 over the two data sets, $P<0.001$). Bite rate, grazing time and total daily bites were all negatively related to intake, and the relationships were much weaker. Only the relationships with grazing time and total daily bites for the complete data set were significant ($r^2 = 0.13$, $P<0.001$; and $r^2 = 0.04$, $P<0.05$ respectively).

This suggested that of the three components of herbage intake - bite weight, bite rate and grazing time - it was bite weight which was the driving force behind the intake response, with bite rate and grazing time having a compensatory effect when bite weight was low. Since bite weight was derived from the intake measurement and therefore the assumption of independence of variables implicit in the statistical techniques was not fully met, there were reservations about exploring the relationship between these two variables. Nevertheless, some justification may be drawn from the fact that since herbage intake is defined as the product of bite weight, bite rate and grazing time, and both bite rate and grazing time (which were measured independently from intake) were negatively related to intake, then the remaining variable, bite weight, must have been strongly positively related to intake.

Although the total daily bites variable was significantly and positively related to both of its component variables, grazing time and bite rate, the latter consistently had the stronger influence (r^2 = 0.80 and 0.77 for the bite rate relationship in the two data sets, compared with r^2 = 0.47 and 0.44 for the grazing time relationship; $P<0.001$ for each correlation). This was to be expected since bite rate ranged by a factor of 2.7 in the complete data set and 2.0 in the subperiod 1 data, whereas the corresponding ranges in grazing time were 1.9 and 1.6 respectively.

The short-term rate of intake was strongly positively related to bite weight (r^2 = 0.77 over the complete data set and 0.83 for subperiod 1, $P<0.001$ in each case). The relationship between rate of intake and its other component, bite rate, was negative and not significant (r^2 = 0.03 and 0.05 for the two data sets). Although these three variables were not measured independently, there was a clear indication that bite weight had the dominant effect on rate of intake, as it had on daily herbage intake.

These results were in close agreement with the general pattern of ingestive behaviour responses identified in previous experiments, substantiating the use of the behaviour measurement techniques. However, relationships between the Kulczynski similarity index and the ingestive behaviour variables indicated some surprising results, as shown in Appendix 7. Normally, diet selection would be expected to penalise at least the bite weight response, but in the current experiment the similarity index was negatively related to herbage intake, rate of intake and bite weight; these variables were greater when diet selection was high. The relationship with bite weight was stronger for the subperiod 1 data (r^2 = 0.37, P<0.001) than for the complete data set where a stage of grazing component was also involved (r^2 = 0.06, P<0.05).

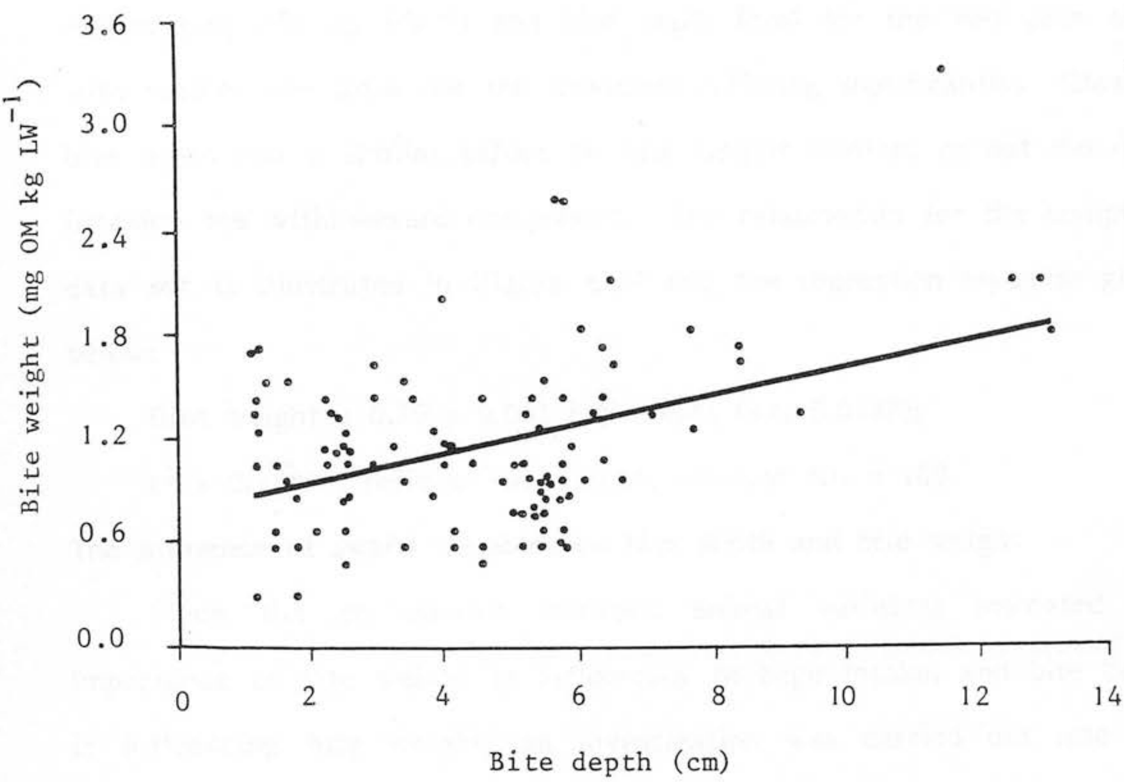
Unlike bite weight, bite rate was positively related to the Kulczynski similarity index and therefore decreased as diet selection increased, as might be expected. The relationship was weaker than the bite weight relationship (r^2 = 0.10, n.s. for subperiod 1; r^2 = 0.04, P<0.05 for the complete data set).

Few previous experiments have investigated the breakdown of the key behaviour variable, bite weight, into its component bite dimensions. This aspect is considered next.

Appendix 7 indicates that bite weight was positively related to bite depth, bite area and bite volume in both data sets, but that the strongest relationship was with bite depth. This applied particularly in subperiod 1 (r^2 = 0.23, P<0.01 for the relationship with bite depth, compared with r^2 = 0.03 and 0.08 for the bite area and bite volume relationships respectively, both n.s.). Although the bite area and bite volume relationships were significant in the complete data set, it was only considered appropriate to apply regression techniques to the bite

Figure E1.7

The relationship between bite weight and bite depth, over the complete data set (n = 102)



weight/bite depth relationship, since only the bite depth dimension was measured independently from bite weight. Indeed, the bite area and bite volume estimates were very approximate as they were derived, ultimately, from the herbage intake measurement itself.

Regression analyses indicated a similar relationship between bite weight (mg OM kg LW^{-1}) and bite depth (cm) for the two data sets, with neither the slope nor the intercept differing significantly. Clearly, bite depth had a similar effect on bite weight whether or not the data included the within-sward component. The relationship for the complete data set is illustrated in Figure E1.7 and the regression equation given below:

Bite weight = 0.79 + 0.081 bite depth (s.e. 0.0182);

r^2 = 0.17***, residual s.d. = 0.46, residual d.f. = 100.

The influence of sward variables on bite depth and bite weight

Since the correlations between animal variables indicated the importance of bite weight in influencing herbage intake, and bite depth in influencing bite weight, an investigation was carried out into the sward variables influencing a) bite depth and b) bite weight.

Bite depth

The correlation matrices in Appendix 7 indicated that bite depth was most strongly and positively related to surface height (r^2 = 0.59 in the complete data set and 0.53 in subperiod 1, P<0.001 for both) and, to a lesser extent, diet digestibility (r^2 = 0.29 and 0.33 respectively, P<0.001). Correlations with leaf depth were weaker than those with surface height, and consequently only surface height was used in further analyses. The diet digestibility variable is considered in greater detail in the Discussion, but as it was probably acting as a dummy for sward properties which were causative in determining the bite depth response, this variable was considered to be important and worthy of further investigation.

Bite depth also appeared to be negatively related to grazed stratum bulk density, although the correlation was only significant over the subperiod 1 data (r^2 = 0.20, P<0.01) and might have been influenced by the strong positive relationship between bite depth and surface height and the weak negative association between height and density.

Multiple regression analysis was used to build up biological models of the variables considered to be driving the bite depth response in the complete data set and in the subperiod 1 data. Table E1.21 contains the important regression equations. When bite depth in the complete data set was related to height, digestibility and the height x digestibility interaction, 0.65 of the variance was accounted for (Equation (1)). The addition of a four-level term for subperiod gave no significant improvement, indicating that the relationship was not significantly affected by the stage of grazing _per_ _se_. Similarly, there was no significant improvement when the subperiod x year interaction was added to test if there was any distortion in the overall relationship from aligning subperiods 1 and 2 in the 1983 data with subperiods 1 and 4 in the 1984 data. The lack of improvement indicated that the differences between the two years in the number and length of the subperiods did not have an undue effect on the bite depth relationship.

The grazed stratum bulk density was not considered to have a major bearing on bite depth. There was no significant improvement when the density term was added to a regression with the x-terms height and digestibility. There was a minor improvement when the density term was added to Equation (1), but the regression coefficient for density became positive which would seem unlikely from a biological viewpoint.

Table E1.21

Multiple regression equations for bite depth and the key sward variables for all data and for subperiod 1

	r^2	Residual s.d.	Residual d.f.
All data			
(1) Bite depth = 5.2 - 1.7 H (s.e. 0.74)- 0.046 D (s.e. 0.107) + 0.024 H.D (s.e. 0.0091)	0.65***	1.51	98
With the addition of CROP	0.78***	1.27	87
CROP and H. Crop	0.84***	1.15	76
Subperiod 1			
(2) Bite depth = 19 - 3.0 H (s.e. 1.46) - 0.21 D (s.e. 0.305) + 0.040 H.D (s.e. 0.0178)	0.73***	1.59	29
With the addition of CROP	0.94***	0.91	18
CROP and H. CROP	0.99***	0.56	7

H surface height (cm) D diet digestibility (IVOMD expressed as a percentage)

H.D height x digestibility interaction H. CROP height x crop interaction

Equation (1) was, however, substantially improved by adding a term for "crop" - when each of the twelve crops was assigned a separate intercept the proportion of variance accounted for increased from 0.65 to 0.78. This figure rose to 0.84 when the slope of the surface height term was also allowed to vary between crops. Clearly crop characteristics other than height and digestibility had an important influence on bite depth, and the relationship with height varied between crops.

Although the relationship between bite depth and the proportion of leaf in the gramineous fraction of the grazed stratum was negative overall (Appendix 7), when individual lines were fitted for each crop nine of the twelve crops had a positive relationship. It was postulated that an increase in sward leafiness might have stimulated a greater depth of head insertion into the sward, but when the leafiness term was added to the full equation described above (r^2 increasing from 0.84 to 0.89) the regression coefficient for the leafiness term was positive for only five of the twelve crops. Clearly the leafiness variable did not have a consistent effect on bite depth, and the relationship might not have been causative.

The bite depth response in the reduced data set, subperiod 1 only, appeared to follow a broadly similar pattern to that for the complete data set. Equation (2) relating bite depth to height, digestibility and the height x digestibility interaction accounted for 0.73 of the variance and was not improved by the addition of grazed stratum bulk density. Adding terms for crop in particular, but also the height x crop interaction, did markedly improve the proportion of variance accounted for, up to a total of 0.99 (Table E1.21).

The proportion of leaf in the gramineous fraction of the grazed stratum was not an important variable in the subperiod 1 data set;

there was no significant improvement from adding the leafiness variable to a regression relating bite depth to crop alone.

In comparing the regressions for the two data sets, it was interesting that neither the intercept nor the slopes of the x-terms differed significantly between Equations (1) and (2). There was, therefore, a consistency in the form of the relationship whether or not the data included the within-sward component. However, the relationship was stronger for the subperiod 1 data. This suggested that in grazing down a sward an additional source of variation was introduced, although the subperiod term did not significantly improve Equation (1). The inclusion of the crop term had a marked effect on both equations, and the height x crop interaction was also important.

Bite weight

Over the complete data set, bite weight, like bite depth, was significantly and positively related to surface height and to diet digestibility (r^2 = 0.20, P<0.001 for each relationship) (Appendix 7). In subperiod 1, the diet digestibility relationship was stronger (r^2 = 0.46, P<0.001) but the height relationship was not significant (r^2 = 0.07). Although the bite weight measurement was not entirely independent from diet digestibility, as the former was derived from intake which was estimated from diet digestibility and faecal output, this association was not considered to be so close that it invalidated further exploration of the bite weight/diet digestibility relationship.

Surprisingly, bite weight was negatively rather than positively correlated with grazed stratum bulk density, the relationship reaching the 0.01 level of significance in the complete data set (r^2 = 0.08) but not in subperiod 1 (r^2 = 0.06, n.s.). A negative causative relationship would be most unlikely biologically, but the relationship also appeared to be negative within virtually all of the individual crops, whether or not the data were restricted to subperiod 1. This unexpected result is considered in more detail in the Discussion.

Although the correlation matrices in Appendix 7 indicate a positive association between bite weight and daylength (r^2 = 0.26 for the complete data set and 0.34 for subperiod 1, P<0.001 for both) this appeared unlikely to have been a major causative relationship for two reasons. Firstly, although as mentioned previously daylength did appear to have the dominant influence on voluntary intake in the indoor feeding trials, the grazing trial correlations indicated that the apparent effect of daylength on herbage intake was mediated solely via bite weight, rather than via grazing time as might be expected. Indeed, the grazing time/daylength relationship was negative.

Secondly, if bite weight did respond directly to daylength, one would expect a significant positive relationship between daylength and bite volume, and therefore also bite area and/or bite depth. Although in this experiment both bite area and bite volume were measures of the dimensions effectively covered by a bite rather than the dimensions limited by mouth dimensions, the lack of a significant relationship between bite depth and daylength throws some doubt on the concept of daylength being a major driving force behind the bite weight response. In view of the uncertainties over the possible mechanism whereby daylength might influence bite weight, daylength per se was not considered further as a potential influence on bite weight.

As with bite depth, biological models of the variables considered to be driving the bite weight response were built up using regression techniques, and the resultant equations are presented in Table E1.22.

Equation (1) shows bite weight related quadratically to diet digestibility, with 0.45 of the variance accounted for. The addition of surface height gave a small improvement (Equation (2); r^2 = 0.49) and

Table E1.22

Multiple regression equations for bite weight and the key sward variables for all data and for subperiod 1

	r^2	Residual s.d.	Residual d.f.
All data			
(1) Bite weight = 146 − 3.7 D (s.e. 0.56) + 0.023 D^2 (s.e. 0.0035)	0.45***	0.37	99
(2) Bite weight = 141 − 3.5 D (s.e. 0.54) + 0.022 D^2 (s.e. 0.0034) + 0.023 H (s.e. 0.0079)	0.49***	0.36	98
(3) Bite weight$_{s1}$ = 142.8; Bite weight$_{s2}$ = 142.5; Bite weight$_{s3}$ = 142.4; Bite weight$_{s4}$ = 142.3; −3.6 D (s.e. 0.49) + 0.022 D^2 (s.e. 0.0031) + 0.0015 H (s.e. 0.0085)	0.59***	0.33	95
With the addition of CROP	0.83***	0.22	84
CROP and D. CROP	0.90***	0.19	73
Subperiod 1			
(4) Bite weight = 160 − 4.0 D (s.e. 1.29) + 0.025 D^2 (s.e. 0.0078)	0.60***	0.37	30
With the addition of CROP	0.94***	0.18	19
CROP and H	0.95***	0.17	18

H surface height (cm) D diet digestibility (IVOMD expressed as a percentage) $D^2 = D \times D$

Bite weight$_{s1}$ = bite weight in subperiod 1, etc D. CROP digestibility x crop interaction whilst grazed stratum bulk density was not additive to Equation (2), the addition of a term for subperiod accounted for a further 0.10 of the variance (Equation (3); $r^2 = 0.59$). This indicated that in addition to sward height and diet digestibility, conditions associated with the stage of grazing had an effect on bite weight. The intercepts fitted for each subperiod varied only very marginally, but there was a consistent fall between successive subperiods.

None of the subperiod x year, digestibility x subperiod, or height x subperiod interactions significantly improved Equation (3). This indicated firstly that the different alignment of the subperiods in the two years of the experiment did not distort the bite weight relationship, and secondly that the slopes of the digestibility and height terms did not differ substantially between subperiods.

By contrast, adding a term for crop which allowed each crop to take a separate intercept improved the proportion of variance accounted for by 0.24, to 0.83. There was an additional improvement from fitting different slopes to the digestibility term for the different crops ($r^2 = 0.90$ in total).

Despite the overall negative relationship between bite weight and the proportion of leaf in the gramineous fraction of the grazed stratum (Appendix 7), scatter diagrams indicated that the relationship was positive within each crop. By fitting parallel lines for the twelve crops, the leafiness variable accounted for 0.65 of the variance in bite weight in the complete data set, but since the leafiness variable was not additive to the full equation described above (Equation (3) plus crop, plus the digestibility x crop interaction), the importance of the leafiness variable in determining bite weight was in some doubt.

In subperiod 1, bite weight was again related in a curvilinear manner to digestibility (Equation (4); $r^2 = 0.60$), but there was no improvement from adding either the surface height or grazed stratum bulk density terms at this stage. With the addition of crop, a further 0.34 of the variance was accounted for, although there was no additional improvement from fitting the digestibility x crop interaction. Surprisingly, the surface height term was additive after the crop term, marginally improving the proportion of variance accounted for from 0.94 to 0.95.

As in the complete data set, bite weight in subperiod 1 was positively related to the sward leafiness variable within crops (r^2 = 0.82, P<0.001 for parallel lines) but the leafiness variable was not additive to the terms used in the full regression equation described above.

A comparison of Equations (1) and (4) indicated that neither the intercept nor the slopes differed significantly; bite weight responded in a similar manner to diet digestibility whether or not the data included the within-sward component. As with the bite depth data, the bite weight relationships were stronger in subperiod 1 than over all data, and a comparatively large proportion of the variance was accounted for by the term for crop.

Discussion

After considering some of the implications of the experimental approach and design and the sward conditions produced, the animal responses in terms of herbage intake, ingestive behaviour and diet selection will be discussed. Finally, the influence of sward variables on the two key bite responses - bite depth and bite weight - will be considered.

Experimental design and sward conditions

The experimental approach was to expand the range of sward conditions available for study outwith the range normally encountered in temperate grazed swards, in order to detect the animal's grazing responses to a wide - and ideally independent - variation in sward height and density. Rather than attempt strict replication of swards, it was decided to aim to produce a broad spectrum of sward conditions. The emphasis was on pinpointing response trends between rather than within swards.

Inevitably, the grazing trials took place over a period of several months in each year of the experiment, but it was hoped to minimise any possible confounding of animal responses with seasonal effects by planning the cropping sequence to ensure that, for example, cereal crops were grazed at both the start and end of the season. In addition, two contrasting crops were grazed as a pair whenever possible.

Two of the cultivars grazed in 1983 were repeated in 1984, but although the intrinsic characteristics of those cultivars, such as taste and chemical composition, might have been expected to be similar in the two years, the canopy structure was not always similar. The barley H sward, for example, was 44.9 cm high with a herbage mass of 4090 kg OM ha^{-1} before grazing in 1983, compared with a height of 29.9 cm and a mass of 1020 kg OM ha^{-1} in 1984 (Table E1.7). Consequently, the twelve crops grazed over the two years of the experiment were all treated as individual crops during the analysis of the results, despite some repeat grazings of crop species and even cultivars.

The indoor feeding trials, originally included in the experimental design in order to identify differences in the intake potential of different crops due to internal plant characteristics, indicated instead that daylength appeared to have the dominant influence on voluntary intake. Whilst it was recognised that daylength was not necessarily the causative seasonal variable, it was the most easily determined and has been found to have a strong bearing on intake in previous experiments (Forbes 1982b, 1986). Nevertheless, as explained in the Results, daylength was not considered to be the major driving force in determining the intake and ingestive behaviour responses in the grazing trials.

Each grazing trial had an eight-day measurement period, unless the crop was grazed down before that time. An eight-day period was chosen as a compromise between a longer period with more gradual changes in sward and animal variables and therefore more easily defined response patterns, and a shorter period with less risk of the complications of substantial crop growth.

The herbage allowance employed to ensure that the herbage in each plot was grazed down to a short stubble over the measurement period took no account of herbage growth during grazing. After setting the allowance too low on the 1983 barley and red fescue crops and having to cut short the measurement period or remove cattle from the plots, a standard initial allowance of 60 g DM kg LW^{-1} was employed and found to be satisfactory in most cases. As a consequence of the constant allowance, plot area and stocking rate varied considerably - for example in October 1984 the barley L plot supported four sheep on 0.53 ha whilst the PRG4 Lg plot of only 0.02 ha was stocked with six sheep (Table E1.2). The effects of trampling and fouling were more severe on the smaller plots, but this was unavoidable.

With the herbage allowance set higher than was originally anticipated, the area of land sown to each crop was insufficient to support the full complement of four cattle and four sheep per plot in 1983. Due to the reduction in cattle numbers, the quality of the cattle data was limited, and consequently the results presented centre on the grazing responses of the sheep. In 1984, plots were stocked with sheep only, normally six rather than four per plot in order to improve the estimates of the animal responses.

Further improvements were implemented in 1984. The number and/or frequency of several sward measurements were increased, and the number of intake subperiods was increased from two to four. Although in 1983 the estimates of faecal output, and hence intake, were likely to be more robust than in 1984 as each combined faeces collection comprised samples from a greater number of days (usually three or four compared with two), the response patterns in intake were better defined in 1984 when there were twice as many subperiods.

The employment of different crops and seed rates at sowing certainly produced a wide range of sward conditions for the grazing trials. In general, plots sown at the highest seed rate had the greatest tiller density and herbage mass, but were also the tallest (Table E1.7). The two plots on each of the two established PRG crops had a contrasting pre-grazing herbage mass, and also surface height in the case of the PRG4. On six of the ten young crops, grazed stratum bulk density in the first subperiod tended to increase within a crop according to sowing density, but it was at variance in the other four crops (Table E1.10).

Despite the wide variation in sward conditions, complete dissociation of the important sward variables was not achieved, even when the data set was restricted to subperiod 1 (the between-sward comparison). In particular, surface height tended to be related negatively to grazed stratum bulk density and positively to diet digestibility.

<u>**Herbage intake, ingestive behaviour and diet selection**</u>

The mean values per plot per subperiod for grazing time, bite rate and total daily bites all fell within the ranges quoted for other experiments on temperate sown swards (Hodgson, 1986). Some of the daily herbage intake values appeared to be high; out of a total of 102 values for the two years of the experiment, twelve values were 40 g OM kg LW^{-1} or more (Table E1.12). Indeed, three values exceeded 50 g OM kg LW^{-1} (maximum 54.6 g OM kg LW^{-1}). There is little confirmatory evidence of such high intakes in the literature, although Forbes and Hodgson (1985a) quoted estimates of up to 48 g OM kg LW^{-1} for sheep and up to 53 g OM kg LW^{-1} for cattle. These authors considered that the high values might have been overestimated. However, in their experiment and in the current trials the highest values occurred at the start of grazing, after animals had been transferred to fresh pasture from relatively hard-grazed swards. Thus, the intake drive would have been high initially, and the high intakes observed might well have been a genuine, although temporary, animal response.

Voluntary intake indoors in Experiment 1 ranged up to only 37 g OM kg LW^{-1}, but intake in the grazing situation would be expected to be higher (Forbes, 1986).

Following on from the high intake estimates in the grazing trials, one bite weight value (3.29 mg OM kg LW^{-1}) and five rate of intake values (ranging from 87.0 to 125.8 mg OM kg LW^{-1} min^{-1}) were greater than the maxima of 2.60 mg OM kg LW^{-1} and 80 mg OM kg LW^{-1} min^{-1} recorded in several previous experiments on temperate sown swards (Hodgson, 1986). Again, the high Experiment 1 values might have been genuine or might have been overestimated, but the overall trends both within and between swards were not in any doubt.

Patterns of response in ingestive behaviour and herbage intake followed the general trends outlined in the Literature Review, with bite weight the main determinant of intake. Bite rate and grazing time tended to increase as bite weight declined, but grazing time on some crops fell towards the end of the trial. Such a response has also been noted, on particularly short or sparse swards, by Arnold (1964), Chacon and Stobbs (1976), Hendricksen and Minson (1980) and Bircham (1981).

The results also indicated the importance of bite depth in determining bite weight. Bite depth was estimated from an assessment of the depth of head insertion into the sward, and its accuracy was limited by the comparatively wide head depth recording bands. In addition, it was not known to what extent the measurement reflected true bite depth (depth of a single bite) rather than grazed depth (depth of several successive bites down the sward profile). Nevertheless, the range of values, from 1.2 to 13.1 cm, was not dissimilar to the range (0.3 - 11.9 cm) obtained by Forbes (1982a) for bite depth measured by detailed sward measurements for sheep grazing swards covering a broadly similar range in height to those in Experiment 1.

Some of the diet selection responses were surprising. Whereas neutral or positive selection indices were found for the green fraction of the gramineous material on all swards, and for gramineous material (as opposed to broad-leaved weed) on the vast majority of swards, on the 1983 red fescue L both sheep and cattle appeared to select for weed and against gramineous material. This could either be a genuine result or a reflection of sampling error in either the extrusa collections or stratified clips.

Although in general sheep and cattle have been found to eat leaf in preference to stem (Arnold, 1981), selection responses for the leaf fraction of the gramineous material were inconsistent in Experiment 1. While 27/72 (1984 sheep), 22/51 (1983 sheep) or 23/50 (1983 cattle) of the leaf selection indices were classified as neutral, and 25/72 (1984 sheep), 7/51 (1983 sheep) or 4/50 (1983 cattle) as positive, the remaining 20/72 (1984 sheep), 22/51 (1983 sheep) or 23/50 (1983 cattle) were negative. This apparent rejection of leaf was not confined to any particular subperiod, and it occurred on a wide range of crops. It might have been a genuine response, although presumably it would be difficult for an animal to graze stem in preference to leaf due to the structure of the grass or cereal tiller.

Alternatively, leaf content might have been overestimated in the grazed stratum or underestimated in the extrusa. An examination of the stratified clip data indicated that the former was a possibility. In deriving the grazed stratum composition it had to be assumed that there was a linear change in the mass of each component between the days on which the clips were taken, but the 1984 data with a clip taken mid-grazing indicated a much sharper fall in leaf mass in the grazed stratum during the first part of the trial than the second. This applied to every sward except PRG1 T and B, which maintained a relatively high leaf content throughout the trial. Presumably in the majority of swards the actual fall in the mass of leaf in the grazed stratum would be curvilinear rather than linear with time. Therefore leaf mass, and hence leaf proportion, would be overestimated by applying the assumption of linearity. This would also explain the more frequent occurrence of apparently negative leaf selection indices in 1983, when there was no mid-grazing stratified clip. In the absence of more frequent stratified clip measurements it was not possible to improve the accuracy of the leaf selection assessment, and the apparently negative responses detected on certain swards should perhaps be treated with some caution.

When the Kulczynski index was calculated as an overall indication of the similarity of the herbage composition of the diet and grazed stratum, bite weight was found to be unexpectedly positively related to diet selection in the sheep. Previous experiments have indicated that an increase in diet selection tends to penalise bite weight (Stobbs, 1973b; Chacon and Stobbs, 1976; Hendricksen and Minson, 1980) but one possible explanation would be that in the current experiment sheep were only willing to select from swards which allowed a relatively large bite weight in the first place. The sheep might not have been prepared to graze selectively on swards which limited bite weight.

The relationship between bite rate and diet selection in Experiment 1 was weak but negative, in line with results obtained by Seip and Bunnell (1985).

Although it was not possible to make a comprehensive comparison between the grazing responses of sheep and cattle, some minor differences were noted. Overall, the median bite depth was slightly greater (by 0.5 cm) for cattle than for sheep, although the simulated maximum depth was greater, by 1.0 cm for sheep. This would agree with the finding of Hafez and Schein (1962), Van Dyne et al (1980) and Forbes (1982a) that sheep may graze closer to the ground than cattle, at least on some swards.

The mean IVOMD was lower by 0.025 for cattle than for sheep, presumably because the cattle diets had marginally lower mean proportions of gramineous material (0.97 vs 0.98) and leaf material in the gramineous fraction (0.66 vs 0.68) than the sheep diets. The mean proportion of green material in the gramineous fraction (0.97) was similar for the diets of both species. Previous work has indicated that cattle diets may contain less leaf than sheep diets from the same sward (Dudzinski and Arnold, 1973; Mulholland et al, 1977; Forbes, 1982a, experiment 3), and sometimes also less green material (Mulholland et al, 1977; Arnold, 1980).

Selection responses across plots and subperiods in the current experiment were broadly similar for the two animal species. Although the Kulczynski similarity indices did indicate that, overall, cattle might have been slightly more selective than sheep, i.e. had a lower index (0.78 vs 0.83), this was probably a reflection of the greater apparent selection by cattle for weed on the red fescue L, and for gramineous stem on several other plots. These responses have already been questioned. In general, the data appeared to indicate a similarity in, rather than a contrast between, the diet selection responses of the sheep and cattle.

The influence of sward and other variables on bite depth and bite weight

It was evident from the multiple regression analyses that the determinants of both bite depth and bite weight of the sheep fell into the following four categories:

1. sward variables
2. subperiod (for the bite weight relationship only)
3. crop
4. unknown.

It was hoped that most of the variance in both of the bite responses would be accounted for by the sward variables measured, perhaps with an additional subperiod effect assuming some importance in the complete data set. Ideally, the crop effect would not be significant once the sward variables had been included in the regressions, but this was clearly not the case, as will be discussed. The first three categories of determinants of the bite responses are considered next.

Of the many sward variables measured, surface height and diet digestibility appeared to be the most important in determining both bite depth and bite weight. Sheep grazed deeper on taller, more digestible swards, and bite weight increased as a consequence.

The effect of diet digestibility may be explained by considering this variable not simply as a measure of the nutritional quality of the harvested herbage, but as a dummy for the wide range of sward properties that vary both between different levels of the sward profile and when comparing contrasting swards and crops. The stratified clip measurements indicated a general increase in the proportions of stem and brown material at lower levels of the sward, and it may be assumed that these were associated with both a decline in the nutritional quality of the herbage and an increase in the stiffness and tensile and shear strengths of the (live) herbage. Thus, the variable named diet digestibility would encompass aspects of sward canopy structure including both sward composition and height, and one might postulate that the sheep might bite down to some threshold "digestibility" level which was determined by quality and/or mechanical properties.

The sheep might judge this threshold level via the senses of sight, smell, touch or taste. From the forces the animal was obliged to exert on the herbage, it might also monitor herbage stiffness, tensile strength and/or shear strength during the harvesting process, and perhaps also shear strength during mastication. This additional information could be used in determining how deep to graze a sward. Presumably the depth of "acceptable" herbage would vary not only with factors relating to the sward canopy structure but also with factors such as the animal's appetite drive. The threshold level, as indicated by the lower limit of the grazed stratum, generally changed with time, declining as a sward was grazed down.

The influence of diet digestibility on grazing responses has also been noted by Hodgson _et al_ (1977) and Illius (1986). In trials on both temperate and tropical swards, Hodgson _et al_ (1977) found that diet digestibility had the major influence on daily herbage intake, although in the tropical swards there was an additional effect due to sward structure variables such as height. Illius (1986) found that diet digestibility could exert a marked effect on bite rate at a given height, and he attributed this to an increase in both searching time and the amount of chewing required on herbage of lower quality (higher shear strength). The current experiment indicates that the bite weight and bite depth variables can also be strongly influenced by diet digestibility.

Responses in bite depth and bite weight to an increase in the leafiness of the grazed stratum were either weak or inconsistent (positive in some crops and negative in others) or the leafiness variable was not additive to the equations using the height and digestibility variables. It would be difficult to determine whether the leafiness of the grazed stratum had an effect on bite depth, or vice versa, without also considering the leaf content of the sward in the layer immediately below the grazed stratum.

The influence on bite responses of one further sward variable, the grazed stratum bulk density, must also be considered. Although there appeared to be a negative relationship between bite depth and grazed stratum bulk density, in line with the observations of Black and Kenney (1984), the confounding of sward variables in the current experiment might have accounted for the relationship. The density variable was either not additive to equations containing x-terms for sward height and digestibility, or its regression coefficient became positive which was most unlikely from a biological viewpoint.

Bite weight appeared to be consistently but weakly negatively related to grazed stratum bulk density in Experiment 1; the relationship was even negative when the data were restricted to subperiod 1 (the between-sward comparison), although it was not statistically significant (r^2 = 0.06). A causative negative relationship would be most unlikely on biological grounds, and again the relationship might have reflected the confounding of density with height and digestibility. Density was not additive to these variables in the multiple regressions. Similarly, Hodgson (1981a) attributed an apparently strong negative relationship between bite weight and grazed stratum bulk density in a series of grazing trials to the confounding effects of sward height.

The lack of a positive relationship between bite weight and grazed stratum bulk density might also have reflected the problems in measuring this sward variable accurately. Although the method used in Experiment 1 was considered to be an improvement over that employed by Hodgson (1981a), at least for the particular sward conditions of the current experiment, it clearly had its shortcomings. More frequent measurements of sward canopy structure would have reduced the reliance upon interpolated profiles, and during and after grazing it might have been better to confine the stratified clips to the grazed areas rather than covering both grazed and ungrazed patches. The animal is unlikely to relate to "mean" sward canopy structure, which in any case may not be represented in the field to any great extent.

In addition to the problems of plot variability - which of course were not unique to the density measurements - the grazed stratum bulk density estimates were further complicated by confounding of the effects of grazing with those of trampling. This is an inherent problem in any grazing situation where the animal is free to walk over the sward.

Furthermore, several of the young crops had a proportion of their tillers uprooted during grazing, and this altered the normal pattern of change in grazed stratum bulk density as a sward was grazed down. Thus, in the majority of swards the grazed stratum bulk density tended to increase in successive subperiods, but in a few swards, notably the 1984 timothy L, M and H, the density fell markedly (Table E1.10).

Although attempts to measure bulk density in the grazed stratum can only be an improvement over measuring mean bulk density for the whole sward (herbage mass divided by surface height), even grazed stratum bulk density may be a crude measurement in many instances. It may not equate with density as perceived by the grazing animal. For example, as a sward is grazed down the grazed stratum bulk density will change from being a measure of the density of predominantly leaf material to that of predominantly stem material. Also, when comparing different swards and crops it may be an oversimplification to quote a single value for grazed stratum bulk density as swards may vary considerably with respect to the population size, weight and relative proportions of leaves and stems. In sparse swards, the spacing between individual plant units or tillers is also likely to be important, and an overall grazed stratum bulk density measurement which includes large gaps between plant units is probably not a good predictor of bite responses.

After fitting x-terms for the key sward variables - surface height, diet digestibility, and whichever quadratic terms or interactions gave a significant improvement - the multiple regression for bite weight over the complete data set was further improved by adding a term for subperiod (Table E1.22) whereas the bite depth regression was not (Table E1.21). Evidently there was a decline in bite weight in successive subperiods over and above the decline due to a fall in sward height and digestibility. Since the grazed stratum bulk density generally increased in successive subperiods, bite volume must have declined as bite weight declined. Furthermore, since there appeared to be no additional effect of subperiod on bite depth over and above the effects of height and digestibility, it would appear that the subperiod effect on bite weight was due to a decline in bite area in successive subperiods.

It is not unreasonable to suggest that the sheep might have reduced bite area as the sward was grazed down; this might have resulted from an increase in the tensile strength of the herbage, or from the sheep selecting increasingly sparse sward components such as green leaf, or perhaps selecting untrampled herbage or herbage uncontaminated by faeces, soil or fungal infection. However, the theory could not be tested in this experiment as true bite area was not measured. The estimates of the area effectively covered by a bite were very approximate and in the sparser swards would have reflected the dispersion of the plant units rather than any adjustment of mouth area by the animal.

The multiple regression equations for bite depth (Table E1.21) and bite weight (Table E1.22) were significantly improved by adding a term for crop after the inclusion of the sward variables and - in the case of bite weight in the complete data set - the term for subperiod. Over the four regressions, the proportion of variance accounted for increased from 0.59 - 0.73 to 0.78 - 0.94 and in three regressions there was a further improvement by including the height x crop or digestibility x crop interaction. The true nature of the crop effect could not, however, be determined. Crop genotype per se might have had some effect, but the indoor trials indicated that it was unlikely to be a major factor. A seasonal element might also have been involved when comparing crops in different trials. A further possibility was that the crop effect was due to a complex combination of the whole range of sward variables measured, or - more likely - was a reflection of unmeasured sward characteristics, such as those suggested above as requiring greater definition than an overall grazed stratum bulk density measurement.

Conclusions

Although a wide range of sward conditions was produced for the study of grazing responses in Experiment 1, it did not prove possible to dissociate completely the key variables; surface height, grazed stratum bulk density and diet digestibility. The overall patterns in ingestive behaviour and daily herbage intake were as expected, and highlighted the importance of bite depth and bite weight in influencing intake. Each of these key bite responses was apparently determined largely by sward height and digestibility, both in the complete data set (within- and between-sward comparisons) and when the data were restricted to subperiod 1 only (the between-sward comparison). Grazed stratum bulk density, however, appeared to have a minor and unexpectedly negative effect on bite weight, and a substantial proportion of the variance in each bite response was attributed to undescribed differences between crops.

The experiment indicated the need for greater experimental control in order to clarify the relationships between grazing responses and sward variables. In particular, a better determination of grazed stratum bulk density was required in order to confirm the importance or otherwise of this variable in determining bite weight.

EXPERIMENT 2

The influence of sward canopy structure on the bite dimensions and bite weight of grazing sheep

Introduction

Both the Literature Review and Experiment 1 highlighted the dominant role normally played by bite weight in determining the daily herbage intake of the grazing ruminant, and yet there has been little previous work on the bite dimension components of bite weight and how they are affected by sward canopy structure. Bite depth or grazed depth has been measured in some experiments, but bite area appears to have been measured only on artificial swards (Black and Kenney, 1984) and bite volume not at all.

In Experiment 1, bite depth was estimated from observations of the depth of head insertion into the sward and was found to be strongly related to both bite weight and certain sward variables. However, estimates of bite area and volume, derived ultimately from measurements of herbage intake, were considered to be too crude for an investigation of the relationships with bite weight and the causative sward variables. Clearly a more critical study of bite dimensions was required.

Experiment 2 was devised to examine in some detail the influence of sward canopy structure on the three bite dimensions and bite weight in sheep. In addition, some aspects of diet selection were investigated. The measurement of bite dimensions was more refined than in the first experiment, the dimensions being calculated directly from detailed sward measurements. The approach allowed a greater degree of experimental control and involved close confinement of sheep to small uniform areas of contrasting swards from which they were allowed to take only 20 bites.

Materials and Methods

Site and location

The experiment was carried out at the Hartwood Research Station of the Hill Farming Research Organisation, in the same two fields as Experiment 1. Details of field conditions are given under Experiment 1. A range of gramineous swards was sampled between July and October 1984, the trials being run between the Experiment 1 trials.

Experimental design

The experimental design was for each of four sheep to sample each of seventeen contrasting swards.

Swards

Table E2.1 lists the seventeen swards in the order in which they were grazed and provides a key to the crop and sward abbreviations used. All crops used in Experiment 2 were also used in Experiment 1 and in general the same plots were used, although the four-year-old perennial ryegrass leys (PRG4) comprised different but similar plots in the two experiments. Details of cultivars, seed rates at sowing and crop husbandry are described under Experiment 1. The swards sampled in Experiment 2 were either fresh, primary growths (oats H, L, M; am. PRG H, M; Agrostis L) or regrowths following grazing (oats MG; timothy HG; PRG4 LgG, SG) or regrowths following cutting with a reciprocating mower at a height of approximately 5 cm (oats HC; am. PRG HC; timothy HC). In addition, certain swards were cut a few days before sampling with battery-operated clippers running along a guide rail set at the required height above ground level. Thus the oats LP, MP, and HP swards were produced by cutting areas of sward in the ungrazed L, M and H plots at a height of approximately 15 cm; and the PRG4 LgP sward was produced by cutting an area of the LgG regrowth at a height of approximately 10 cm. The aim was to ensure a very wide

Table E2.1

Swards sampled in Experiment 2 in 1984, listed in chronological order

Sampling date	Trial	Crop[a]	Sward[b]	Time since sowing	Preliminary treatment	Days since treatment
31 July	1	oats	H	11 weeks	none	-
			L		none	-
			M		none	-
1 Aug.	1	oats	LP		hand-cut	1
			MP		hand-cut	1
			HP		hand-cut	1
2 Aug.	1	oats	MG		grazed	11
			HC		cut	15
29 Aug.	2	am. PRG	H	18 weeks	none	-
			M		none	-
			HC		cut	12
25 Sept.	3	Agrostis timothy	L	20 weeks	none	-
			HG		grazed	37
			HC		cut	41
2 Oct.	4	PRG4	LgP	4 years	hand-cut	5
			LgG		grazed	not known
			SG		grazed	19

a am. PRG : perennial ryegrass cultivar normally sown on amenity areas
PRG4 : perennial ryegrass established for four years

b L, M, H : swards sown at low, medium or high seed rates
Lg, S : long and short swards
P : swards pre-cut using hand-held clippers
G, C : regrowths following grazing (G) or cutting with reciprocating mower (C)

range in sward canopy structure and some independant variation in sward height and density.

Whenever a cutting treatment was employed, all cut herbage was removed from the sward before sampling.

Animals

Four Scottish Blackface wethers, fistulated at the oesophagus, were used in the trials. They were two years old at the start of the 1984 grazing season and as they had been used in Experiment 1 in 1983 were quite tame and accustomed to being handled. Between trials they were maintained on a short established PRG sward. Routine health care is outlined in Appendix 3.

Experimental procedures

During sampling of a sward, each sheep was confined in a modified metabolism crate which allowed access to an area of sward 0.56 x 0.46m. Figure E2.1 shows a sheep grazing in one of the cages. Access into the cage was through a door at the back and the sheep was not tethered in any way. It stood on the mesh floor just above ground level and was only constrained in its movements by the solid walls surrounding the floored part of the cage and by the wire-netting on the wooden frame surrounding the patch of herbage to be grazed (the "cage patch").

Before the cages were positioned over the experimental sward, narrow strips of herbage were removed from the outer edges of the cage patches to ensure that no herbage rooted outside the patches could protrude in through the netting. On each sward a uniform strip of herbage approximately 4 m long was required to accommodate, in one row, four cage patches plus extra areas for certain post-sampling sward measurements (Figure E2.2).

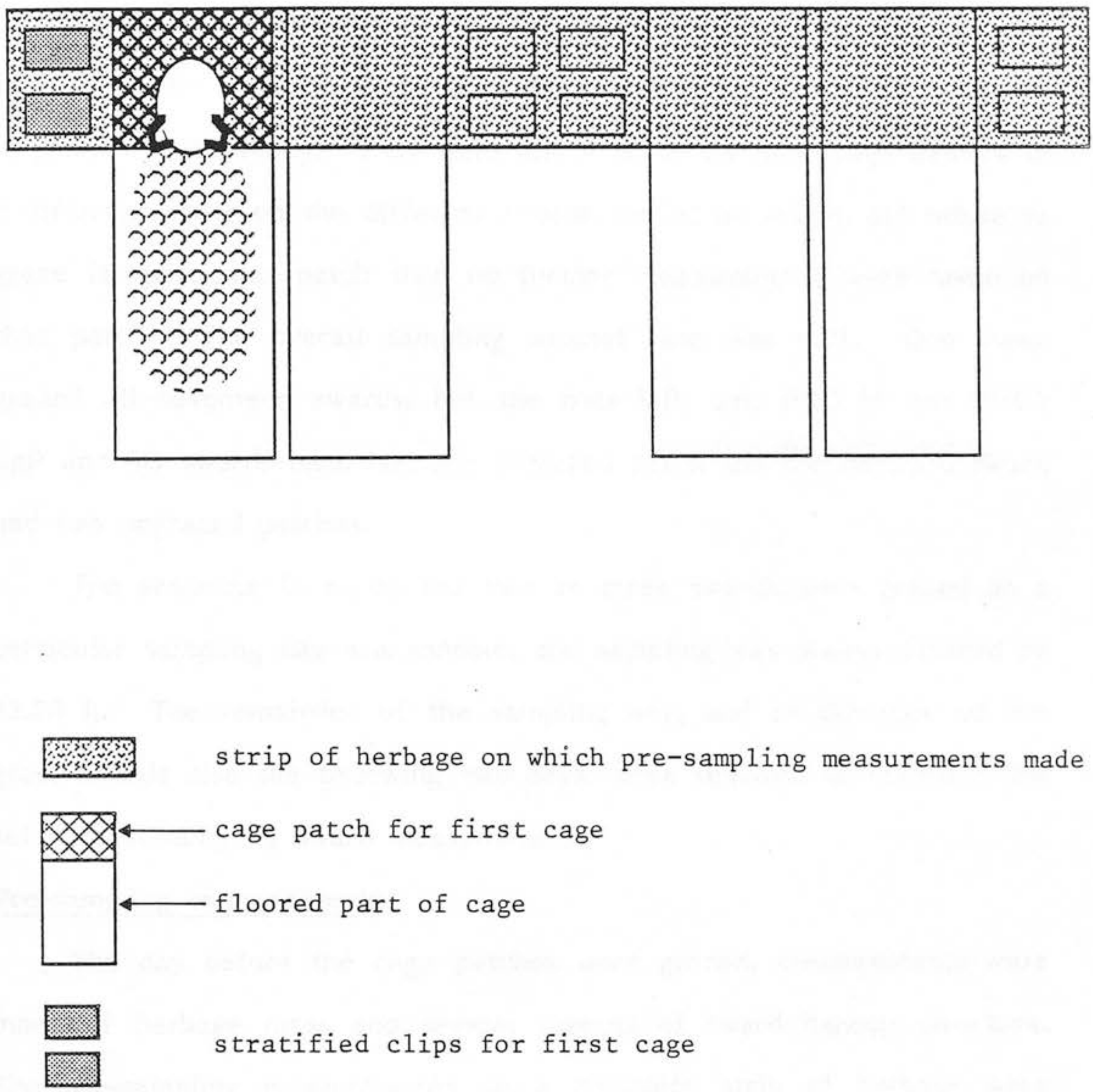
In order to standardise animal preparation the sheep were penned with water but without food from 17.00 h the evening before grazing

Figure E2.1

An oesophageal fistulated sheep, confined in a grazing cage, sampling a pre-cut sward (oats LP)

Figure E2.2

Plan view of the experimental layout on a typical sward



until sampling began the next day at 09.00 h. During sampling, a sheep was fitted with a foam rubber plug in the oesophagus below the fistula and then allowed to take 20 bites from its cage patch. All extrusa were collected in a polythene bag tied round the animal's neck.

The sheep were well accustomed to grazing within the confines of the cages, had previous grazing experience of the various crops, and were generally keen to start eating regardless of whether they were run in pairs or individually. They were allocated to the four cage patches in a different order on the different swards, and if an animal did refuse to graze its particular patch then no further measurements were taken on that patch. The overall sampling success rate was 0.91. One sheep grazed all seventeen swards, but the oats MP, am. PRG M and PRG4 LgP and SG swards each had one ungrazed patch and the oats MG sward had two ungrazed patches.

. The sequence in which the two or three swards were grazed on a particular sampling day was random, and sampling was always finished by 12.00 h. The remainder of the sampling day, and in the case of the grass swards also the following two days, were required to complete the set of post-sampling sward measurements.

Pre-sampling measurements

The day before the cage patches were grazed, measurements were made of herbage mass and several aspects of sward canopy structure. The pre-sampling measurements on a complete strip of herbage were assumed to represent the conditions within each of the four cage patches.

Herbage mass. Herbage mass was estimated from two cuts to ground level, each over an area 3.50 x 0.07 m, on rooted herbage adjacent to the cage patches. Battery-powered clippers were used and any roots remaining on the cut herbage were removed. It was then washed and oven-dried at 90°C for at least twelve hours before weighing.

Sward maturity and tiller density. Using the same procedures as in Experiment 1, sward maturity was assessed and tiller density estimated for each sward from a subsample of 50 tillers taken at random from herbage cut from the outer edges of the cage patches.

Sward height. On each strip of herbage, the HFRO sward stick was used to take a minimum of 50 measurements of the height of the undisturbed crop surface (recorded as "leaf", i.e. lamina; stem; or flower). This allowed the calculation of mean surface height (using all measurements) and mean surface leaf height (using only leaf measurements).

Stem height was defined as in Experiment 1. It was the height of the ligule of the youngest fully-expanded leaf on an ungrazed vegetative or immature reproductive tiller; the height of the top of the flower on an ungrazed flowering tiller; or the height of the severed stem on a tiller which had been grazed or cut. Stem height was measured by sward stick or ruler on the same tiller as surface height. The two measurements coincided when the surface contact was stem or flower. Mean stem height was calculated from a total of 50 measurements per sward.

Leaf depth. Mean leaf depth was defined as the difference between mean surface leaf height and mean stem height. Consequently the value obtained could be positive or negative.

Vertical distribution of herbage components. Inclined (32.5°) point quadrats were used to assess the frequency of distribution of the different herbage components within the sward profile. A minimum of 120 herbage contacts were recorded per sward, using the following five categories : crop green leaf (lamina), brown leaf, stem and flower; and weed (weed grass or broad-leaved weed). After ground zero correction, the data expressed as the number of contacts per 100 loci per cm of sward height were set out graphically to illustrate the vertical distribution of herbage components in the sward. Herbage contacts were recorded within 1 cm bands but illustrated in bands ranging from 1 cm on the shortest swards to 5 cm on the tallest swards. The number of bands per graph was kept as constant as possible and ranged from eight to fourteen.

Measurements during sampling

Bite weight. During sampling of a cage patch, a count was kept of the number of harvesting bites taken by the sheep. The required 20 bites were usually achieved. The animal was then restrained from further grazing and the bag of extrusa removed, stored at -18°C and subsequently weighed before and after being oven-dried at 90°C.

Knowing the fresh weight and DM content of the extrusa, assuming the DM content of the stratified clips (See Post-sampling measurements) to represent that of the grazed herbage, and taking the DM content of saliva to be 0.0116 as in Appendix 5, the fresh extrusa weight was corrected for saliva contamination using Equation (2) in Appendix 5. After converting this corrected extrusa weight into DM terms, the mean bite weight (mg DM) was calculated by dividing by the number of bites. Such estimates of mean bite weight are subject to variability in the recovery of ingested herbage (Appendix 5).

Post-sampling measurements

All sward measurements taken after the experimental grazings were on an individual cage patch basis. Within each cage patch, only those leaves, stems or flowers showing signs of having been recently grazed were measured, and these grazed plant units were classified either as leaves (laminae) or stems (pseudostems, flowering stems or flowers). Grazed plant units were distinguished from plant units which had been previously cut or grazed by the appearance of the severed surface.

As certain measurement procedures were different on the relatively sparse oats swards and the denser grass swards, the measurements on the two contrasting forage types will be described separately.

Oats swards

Proportion of leaves and of stems in the grazed plant units. A count of the number of leaves and stems with recently grazed surfaces allowed the calculation of the proportion of leaves and the proportion of stems in the grazed plant units in each cage patch.

Number of grazed plant units per bite. The mean number of plant units severed at a bite was estimated by dividing the total number of grazed units per cage patch by the number of bites.

Grazed height. The height of each grazed plant unit was measured with a ruler and the mean grazed height of leaves, of stems, and of all plant units was calculated.

For each cage patch, a single stratified clip over an area 0.25 x 0.15 m was taken at the overall mean grazed height (rounded to the nearest cm) from each of two adjacent unsampled patches of herbage. Figure E2.2 shows the location of the stratified clips relative to the cage patches. As with the grazed plant units, the cut plant units were classified as either leaves or stems, and the clipped material was used for four main measurements:

a. Proportion of leaves and of stems in the cut plant units. The proportion of leaves and of stems in the cut plant units was calculated after counting the numbers of leaves and stems which had been cut in the combined clips relating to a particular cage patch.

b. Bite area. The mean area in a horizontal plane effectively covered by a bite was estimated as follows:

$$\text{Bite area } (cm^2) = \frac{\text{number of grazed plant units per bite}}{\text{number of cut plant units per clip}} \times \text{area of clip } (cm^2)$$

c. Population density of grazed plant units. This was estimated as follows:

$$\text{Population density of grazed plant units (no. } cm^{-2}) = \frac{\text{number of cut plant units per clip}}{\text{area of clip } (cm^2)}$$

d. Grazed stratum bulk density. The mean bulk density (mg DM cm^{-3}) of the sward stratum grazed by the sheep was estimated by dividing the oven-dried weight of herbage from the stratified clips by the volume occupied in the sward by the clips. The volume of the clips was estimated as the product of the ground area cut and the difference in the pre-sampling mean surface height and the height at which the clips were taken.

Bite depth. Mean bite depth was estimated from the difference between the pre-sampling mean surface height and the mean grazed height.

Bite volume. The mean volume within the sward effectively covered by a bite was estimated from the product of bite depth and bite area.

Grass swards

The major difference between measurements on the grass and oats swards was that meaningful measurements of bite area and the population density of grazed plant units could be made directly on the cage patches for the grasses. Unlike the oats swards, the comparatively dense herbage showed up the extent of the grazed areas.

In each cage patch on a grass sward, those areas which had been grazed were outlined first with a series of long needles pushed into the ground and then with plastic-coated wire formed into the appropriate shapes and placed on the sward surface (Figure E2.3). The recently grazed leaves and stems were counted and the proportion of leaves and of stems in the grazed plant units and the mean number of grazed plant units per bite calculated as on the oats swards. A graduated needle was used to measure the height of a subsample of the grazed units (minimum

Figure E2.3

A cage patch, viewed from above, on the PRG4 LgP sward

The wire shapes indicate the grazed patches used to estimate mean bite area. The wooden boards and scale indicate the edge of the cage patch.

of 54 height measurements on a cage patch) and the mean grazed height of leaves, of stems and of all plant units was estimated.

Next, the wire shapes were lifted from the sward, placed on paper and drawn round to give a permanent record of the shape of the grazed patches. These paper "patterns" were subsequently cut out and put through a bench planimeter to determine their areas. Mean bite area was then estimated from the total area of the grazed patches divided by the number of bites, and the mean population density of grazed plant units estimated by dividing the total number of grazed units by the total area of the grazed patches.

Stratified clips on the grass swards were used only to assess the mean grazed stratum bulk density, with the methodology similar to the oats swards. Mean bite depth was again estimated from the difference in the pre-sampling mean surface height and the mean grazed height, and mean bite volume was the product of mean bite depth and area.

Additional animal measurements

Live weight. The sheep were weighed, to the nearest 0.5 kg, at regular intervals over the summer.

Dentition and mouthpart dimensions. The sheep's teeth were checked at intervals over the summer. Of the three animals which had no tooth changes, two had three pairs of permanent incisors whilst one had two pairs. The fourth sheep had only five permanent incisors during Trial 1 but the sixth incisor had erupted by Trial 2 and was in the cutting position by Trial 3.

On 23 August 1984, various measurements of mouthpart dimensions were made using calipers or a ruler. The measurements included:

a. incisor width - the spread across the incisors;

b. muzzle width - the distance between the corner of the lips on either side of the muzzle, with the mouth closed;

c. lip length - measured on the left side of the face, from the tip of the muzzle to the corner of the lips, with the mouth closed;

d. the maximum width of the open mouth, from the cutting edge of the incisors on the lower jaw to the dental pad on the upper jaw (the sheep's mouth was opened as far as the animal would allow).

Measurement a was made to the nearest 0.1 cm, b, c, and d to the nearest 0.5 cm as they had less clearly identifiable reference points.

Statistical analyses

For the purposes of statistical analysis, the four sheep were considered as blocks and the seventeen swards as treatments. All bite and sward measurements made on an individual sheep (individual cage patch) basis were subjected to analysis of variance, and treatment mean values corrected for any missing values were obtained.

These values were included in a data set with values for the sward characteristics measured over all four cage patches before grazing. These data were used in correlations and regressions relating differences in sward canopy structure between swards to animal responses in terms of bite dimensions and bite weight. Where multiple regressions were employed, successive x-terms were included if they significantly reduced the residual sum of squares.

Analyses of variance based on individual cage patch values were also used to examine aspects of diet selection, after the data on horizontal selection (which comprised proportions or an index with a potential range from 0 to 1) had been subjected to arcsine transformation. Although levels of significance were calculated on the transformed data, the standard errors quoted (Table E2.9) were obtained from a parallel analysis on untransformed data. Data on the proportion of stems in the grazed plant units (Table E2.8) were also analysed in this manner.

All statistical analyses were run on the GENSTAT programme (Lawes Agricultural Trust, copyright 1984), using the facilities of the Edinburgh Regional Computing Centre.

Results

After presenting data on the sward conditions and bite measurements for the seventeen swards, the relationships between the various sward measurements, bite dimensions and bite weight will be explored and then some aspects of diet selection investigated.

Sward conditions prior to sampling

The combination of crops, sowing densities and preliminary treatments provided a wide range of sward conditions for the study. Table E2.2 summarises the main sward characteristics prior to grazing.

The grass swards were predominantly vegetative; although in some cases reproductive tillers were present, none of these had emerged flowers. By contrast, the oats swards all had a relatively high proportion of reproductive tillers, and in those swards which had not been previously cut or grazed (oats H, L and M) on average nearly a quarter of the total tillers had emerged flowers. The maturity of the reproductive tillers in the other oats swards could not be determined as the tops of the stems had been removed during preliminary treatments.

Over all seventeen swards, tiller density ranged sixty-fold, from 600 to 36000 tillers m^{-2}, while herbage mass ranged fourteen-fold, from 300 to 4200 kg DM ha^{-1}. The mean surface height of the oats swards ranged from 7 cm with a corresponding leaf depth of 3 cm, to 55 cm with a corresponding leaf depth of 0 cm, but on the grasses the range of heights was smaller with the lowest surface height 6 cm (leaf depth 4 cm) and the greatest surface height 22 cm (leaf depth 14 cm). On the grass swards the surface contacts were always leaf, and consequently mean surface leaf height (which equalled mean surface height) was

Table E2.2

Sward maturity, tiller density, herbage mass, surface height, stem height and leaf depth prior to sampling

Trial and month	Crop	Sward	Maturity (mean proportion of reproductive tillers)	Tiller density (no. m^{-2})	Herbage mass (kg DM ha^{-1})	Surface height (cm) mean[a]	Surface height (cm) s.e.	Surface height measured on leaves (l), stems (s) or flowers (f)	Stem height (cm) (n = 50) mean	Stem height (cm) (n = 50) s.e.	Leaf depth (cm) (n=50 where s.e. presented) mean	Leaf depth s.e.
1 July/Aug.	oats	H	0.90	1550	4220	55.2	1.28	lf	48.0	2.39	0.03	-
		L	0.78	630	1740	37.5	1.34	lf	30.3	1.85	3.1	-
		M	0.88	940	3720	49.1	1.36	lf	39.7	2.34	3.9	-
		LP	0.82	830	1220	16.6	0.25	ls	16.9	0.22	-0.6	-
		MP	0.82	850	1040	15.1	0.23	ls	15.5	0.31	-0.8	-
		HP	0.78	2020	2270	16.0	0.24	ls	15.7	0.22	0.6	-
		MG	0.70	980	300	6.8	0.43	ls	4.7	0.29	3.3	-
		HC	0.76	2680	1600	22.1	0.78	lf	14.2	0.70	7.8	-
2 Aug.	am. PRG	H	0.00	11210	3490	11.5	0.42	l	3.5	0.18	8.0	0.41
		M	0.00	6940	3530	12.6	0.32	l	4.4	0.18	8.2	0.33
		HC	0.22	10700	1920	7.4	0.28	l	3.4	0.15	4.0	0.25
3 Sept.	Agrostis	L	0.44	21860	2620	12.8	0.40	l	7.2	0.31	5.6	0.40
	timothy	HG	0.06	2250	360	10.8	0.56	l	3.0	0.14	7.8	0.51
		HC	0.02	5370	1470	15.0	0.57	l	7.1	0.25	7.9	0.62
4 Oct.	PRG4	LgP	0.00	23050	2350	11.5	0.24	l	5.8	0.16	5.7	0.18
		LgG	0.00	17780	3790	22.1	0.36	l	8.6	0.26	13.5	0.43
		SG	0.02	36100	1730	5.7	0.17	l	1.7	0.11	4.0	0.18

a n = 50 except for oats LP, MP, HP where n = 95.

greater than mean stem height, giving a positive leaf depth. On each of the oats swards, however, some of the surface contacts were stem or flower, and therefore mean surface leaf height did not equal mean surface height. Depending on the relative magnitude of mean surface leaf height and mean stem height, mean leaf depth might be positive or negative. In Table E2.2, the standard error of the mean leaf depth is presented for each of the grass swards but not for the oats swards as these did not have a full set of pairs of measurements of surface leaf height and stem height on the same tiller.

The vertical distribution of crop green leaf, brown leaf, stem and flower, and weed material, measured by point quadrat for each of the seventeen swards, is illustrated in Appendix Figures E2.1a-q. Irregularities in the overall patterns of distribution of particular components through a profile were probably due to the limited number of contacts within each band, but it was decided not to bulk the data into deeper bands or use any smoothing technique.

Sward measurements recorded after sampling, bite dimensions, bite weight and mouth dimensions

Measurements of sward characteristics determined after sampling, bite dimensions and bite weight are presented in Table E2.3. The sward means for each variable are the means for the four sheep, corrected for any missing values.

The bulk density of the grazed stratum ranged twenty-fold over all seventeen swards and varied between 0.1 and 0.8 mg DM cm^{-3} on the oats and between 0.3 and 2.1 mg DM cm^{-3} on the grasses. The population density of grazed plant units varied by a factor of 50 over the complete range of swards and the ranges over the oats and grasses were respectively 0.04 to 0.16 and 0.68 to 2.08 grazed plant units cm^{-2}.

Table E2.3

Grazed stratum bulk density, the population density of grazed plant units, bite dimensions and bite weight

Trial and month	Crop	Sward	Grazed stratum bulk density (mg DM cm^{-3})	Population density of grazed plant units (no. cm^{-2})	Bite depth (cm)	Bite area (cm^2)	Bite volume (cm^3)	Bite weight (mg DM)
1	oats	H	0.65	0.07	18.1	20.5	360	296
July/Aug.		L	0.58	0.04	12.9	36.8	495	329
		M	0.65	0.08	21.0	16.6	338	275
		LP	0.81	0.12	6.3	9.3	64	87
		MP	0.70	0.13	5.4	18.9	103	80
		HP	0.75	0.16	5.0	13.0	65	113
		MG	0.10	0.05	1.9	29.5	63	56
		HC	0.28	0.08	7.2	33.1	219	122
2	am. PRG	H	1.26	0.80	3.3	20.7	66	125
Aug.		M	1.35	0.68	2.7	21.5	58	148
		HC	0.48	1.00	2.5	15.8	39	74
3	Agrostis	L	2.07	1.77	2.7	21.8	62	158
Sept.	timothy	HG	0.32	1.32	5.6	9.4	53	93
		HC	1.61	0.86	4.3	16.5	71	149
4	PRG4	LgP	0.51	2.08	2.8	18.3	47	40
Oct.		LgG	0.59	0.92	5.6	20.1	109	120
		SG	0.65	1.51	1.1	13.7	10	40
overall mean			0.79	0.69	6.4	19.7	131	136
s.e. of sward means[a]			0.148	0.103	1.17	3.05	37.3	16.1
significance of differences								
between swards			***	***	***	***	***	***
between sheep			n.s.	n.s.	**	n.s.	n.s.	**

a The s.e. presented is an average value; when there are large differences in the size of table entries it may not be appropriate to each entry.

The range in values for bite dimensions over the oats and grass swards respectively were: for bite depth, 2 to 21 cm and 1 to 6 cm; for bite area, 9 to 37 cm^2 and 9 to 22 cm^2; and for bite volume, 60 to 500 cm^3 and 10 to 110 cm^3. Overall, bite weight (estimated from extrusa collection) varied by a factor of eight and ranged from 60 to 330 mg DM on the oats and from 40 to 160 mg DM on the grasses.

Although analyses of variance indicated highly significant differences between swards for each of these sward and bite measurements ($P<0.001$), only for bite depth and bite weight were there significant differences between sheep ($P<0.01$). One of the four animals (sheep 4) tended to take shallower bites (mean bite depth 4.6 cm compared with 6.8, 6.8 and 7.4 cm for sheep 2, 3 and 1 respectively; s.e. of sheep means 0.57) which presumably was the reason why its bites were also lighter (mean bite weight 110 mg DM compared with 147, 146 and 139 mg DM for the same four individuals respectively; s.e. of sheep means 7.83).

As a check on bite weight estimated from extrusa collection (BWe), bite weight was also estimated from sward measurements (BWs) by multiplying mean bite volume by mean grazed stratum bulk density for each cage patch. The relationship between the two independent estimates of bite weight (mg DM) was described by the following linear regression equation:

$BWe = 68 + 0.79\ BWs$ (s.e. 0.069);

$r^2 = 0.69$***, residual s.d. = 50.6, residual d.f. = 60.

The intercept was significantly greater than zero and the slope significantly less than one. It was concluded that although the extrusa-based estimate of bite weight tended to be higher than the sward-based estimate over the range of bite weights studied, the two were strongly related and, considering the large potential for measurement error in each of the variables, were in reasonably close agreement. The extrusa-based estimate of bite weight was used in all subsequent analyses.

The four sheep weighed 58.5, 84.0, 69.0 and 76.0 kg respectively on 9 July 1984. The animal taking the shallowest and lightest bites also had the lowest body weight. Each animal gained between 6 and 10 kg over the twelve week period until 1 October, but this was probably largely due to an increase in body fatness. Despite the differences in live weight between sheep, incisor width measured on 23 August varied only between 3.1 and 3.4 cm (Table E2.4). As incisor width is probably the animal measurement with most influence on bite dimensions and bite weight, it was not considered appropriate to express bite weight relative to live weight.

Besides incisor width, Table E2.4 shows other mouth dimensions measured on the four sheep. While the mean and between-sheep range in values are given for incisor and muzzle widths and lip length, only the maximum width of the open mouth is given (the value obtained from the most co-operative sheep). Theoretical mouth areas and volumes were calculated by multiplying various combinations of mouth measurements together, with 5 cm being taken as the width of the open mouth for each of the sheep.

A comparison was drawn between the bite dimensions (Table E2.3) and the measured and theoretical mouth dimensions (Table E2.4). The maximum bite depth was 21 cm (on oats M) but this was probably not directly related to any mouth dimensions. Such long herbage might well be folded within the mouth, and in addition sheep grazing oats swards were often observed to sever herbage and then draw in material hanging out of the mouth with a series of manipulatory bites or nibbles. However, this method of grazing was rarely observed on the grass swards where the maximum bite depth of 5.6 cm was in line with a mean lip

Table E2.4

Mouth dimensions of the four sheep used in Experiment 2, measured on 23 August 1984

Measurement (cm)	Mean	Minimum	Maximum
Incisor width (I)	3.2	3.1	3.4
Muzzle width (M)	5.4	5.0	6.0
Lip length (L)	5.9	5.5	6.5
Width of open mouth (W)	-	-	5.0
Theoretical mouth area (cm^2)			
a. I x W	16.1	15.5	17.0
b. M x W	26.9	25.0	30.0
Theoretical mouth volume (cm^3)			
a. I x W x L	95	85	107
b. M x W x L	158	138	180

length of 5.9 cm, although it could not be determined whether this was coincidental or causative.

Comparisons of theoretical mouth areas and volumes with sward mean bite areas and volumes were only valid on the grass swards. Only the grasses had a sufficiently high density of plant units for bite area and volume to be likely to reflect the corresponding mouth dimensions. Bite area on the grasses did not exceed 21.8 cm^2, although several values were close to this. Theoretical mouth area, calculated as the product of incisor width and the maximum width of the open mouth, was less than the apparent maximum bite area, at 16.1 cm^2. However, the difference could easily be accounted for by any gathering action by the sheep before severing a mouthful of grass. This would enable the animal to harvest in one bite a patch of herbage covering (before and after it was gathered into the harvesting position) a greater area than the sheep's mouth area. It is also possible that the width of the open mouth during grazing was underestimated and that true mouth area was of a similar magnitude to bite area.

Mouth area calculated as the product of muzzle width and the width of the open mouth (mean 26.9 cm^2) is also tabulated for comparison, but although external mouth measurements such as muzzle width are likely to influence grazing mechanics, the previous definition of mouth area involving measurement of the cutting surface is considered more pertinent to a comparison with bite area.

Similarly, the measurement most likely to reflect bite volume is mouth volume a in Table E2.4; the product of incisor width, width of the open mouth and lip length. The mean value (95 cm^3) was exceeded only by the bite volume on the tallest of the grass swards, PRG4 LgG (109 cm^3). The next largest bite volume was only 71 cm^3, on timothy HC. The difference on the PRG4 LgG sward between bite volume and mouth volume might be explained largely by the increased scope for gathering this tall herbage compared with the shorter swards.

The interrelationships between sward variables, bite dimensions and bite weight

Sward mean values for surface height, leaf depth, herbage mass, tiller density, grazed stratum bulk density, the population density of grazed plant units, bite depth, bite area, bite volume and bite weight were used to investigate the relationships between:

1. the various sward characteristics;
2. sward variables, bite dimensions and bite weight.

The relationships were examined initially by means of scatter diagrams and correlation matrices for either all seventeen swards or the fourteen swards excluding the three tall oats swards (H, L and M). Using this data subset indicated how the relationships changed when only the shorter swards were considered. Finally, the more important relationships within each data set were subjected to regression analysis.

Interrelationships between sward variables

The correlations indicated a weak, non-significant relationship between surface height and leaf depth (r^2 = 0.05 over all seventeen swards and 0.08 over the fourteen swards). Since relationships with the various bite measurements were much stronger for surface height than for leaf depth, attention was concentrated on surface height although the possible effect of leaf depth on grazing mechanics is discussed later.

As expected, surface height and herbage mass were positively related, although the correlation was only significant over all seventeen swards (r^2 = 0.29, $P<0.05$) and not over the fourteen swards (r^2 = 0.08). Surface height was generally poorly correlated with any of the sward density variables (tiller density, grazed stratum bulk density or the population density of grazed plant units) and only the last correlation was significant, over all seventeen swards (r^2 = 0.26, P<0.05). Correlations with grazed stratum bulk density were particularly low (r^2 = 0.01 over the seventeen swards and 0.04 over the fourteen swards, both n.s.). These relationships indicated a good degree of dissociation between sward height and density over the range of swards studied, suggesting that the choice of swards and pre-treatments did provide conditions conducive to isolating the independent effects of height and density on bite dimensions and bite weight.

Interrelationships between sward variables, bite dimensions and bite weight

Of all the sward variables used in the correlation matrix for the seventeen swards, surface height gave by far the strongest correlations with bite depth, bite volume and bite weight. Over the fourteen swards, surface height remained the sward variable most highly correlated with bite depth and volume, but grazed stratum bulk density had a higher correlation with bite weight. The surface height/bite weight correlation just failed to reach the 0.05 significance level. Table E2.5 gives the relevant correlations and their levels of significance, for both the seventeen and fourteen swards.

It should be noted that any analysis attempting to relate bite depth to surface height was imperfect since height was itself used in the calculation of bite depth. This meant that the assumption of independence of variables implicit in the statistical techniques was not fully met, but in the absence of entirely independent estimates of these variables the relationship was explored. Some justification was drawn from the fact that the independently-derived variable grazed height was extremely strongly related to surface height (r^2=0.98, P<0.001 and r^2 = 0.92, P<0.001 on the seventeen and fourteen swards respectively). Attention was, however, focused on bite depth rather than grazed height

Table E2.5

Correlation matrices for the key relationships for a. all seventeen swards and b. fourteen swards, excluding the three tall oats swards

a. d.f.= 15

grazed stratum bulk density	-0.12				
bite depth	(0.97***)	-0.19			
bite area	0.24	-0.13	0.15		
bite volume	(0.89***)	-0.21	(0.86***)	(0.56*)	
bite weight	0.88***	0.15	0.84***	0.40	0.90***
	surface height	grazed stratum bulk density	bite depth	bite area	bite volume

b. d.f.= 12

grazed stratum bulk density	0.06				
bite depth	(0.84***)	-0.21			
bite area	(0.21	-0.09	-0.04		
bite volume	(0.78***)	-0.20	(0.72**)	(0.64*)	
bite weight	0.52	0.72**	0.29	0.18	0.34
	surface height	grazed stratum bulk density	bite depth	bite area	bite volume

Notes: Correlation coefficients in parentheses denote relationships between variables which were not measured independently.
Correlation coefficients for which the level of statistical significance is not indicated are not significant ($P \geqslant 0.05$).

as it was the bite dimension which was of interest.

There were similar reservations about exploring the relationship between bite volume and surface height. However, since bite weight can be defined as the product of bite volume and the grazed stratum bulk density, then if bite weight is strongly related to surface height (as it was for all seventeen swards, if not for the fourteen) the effect of height must be mediated via bite volume (and therefore via either bite depth or bite area). It has already been established that surface height was not strongly related to other sward variables, and therefore the bite weight/surface height relationship was not simply a reflection of the relationship between bite weight and, for example, grazed stratum bulk density.

Unlike the other bite measurements, bite area was not significantly correlated with any sward variables, including surface height and grazed stratum bulk density (Table E2.5). Nevertheless, the correlations with height or herbage mass were positive whilst those with each of the density variables were consistently negative, over the seventeen and the fourteen swards.

The correlations between bite measurements, presented in Table E2.5, indicated strong relationships between bite weight and both bite volume and bite depth for the seventeen swards, but much weaker (non-significant) relationships over the fourteen swards. Clearly, the strength of both these relationships depended to some extent on the inclusion of the three tall oats swards.

By contrast, the positive relationship between bite weight and bite area was not significant for either data set. Bite depth and bite area were also weakly correlated but bite volume was significantly positively related to both of these bite dimensions, over both data sets. The correlation with bite depth was higher in each case, indicating that this variable had the greater influence on bite volume. However, since bite volume was derived directly from measurements of bite depth and area, it was not considered appropriate to investigate these relationships further.

The regression lines for the relationships between bite depth and surface height, bite volume and surface height, bite weight and bite depth, bite weight and bite volume, and bite weight and surface height (seventeen swards) and between bite weight and grazed stratum bulk density (fourteen swards) are illustrated in Figure E2.4 to E2.9 respectively. The regression equations are given in Table E2.6. None of these relationships between two variables showed evidence of a significant deviation from linearity, nor of a significant improvement from fitting regression lines for the oats and grasses separately.

Equations (1), (2) and (5) were examined to determine whether the addition of a term for herbage mass, tiller density, grazed stratum bulk density or the population density of grazed plant units gave a significant improvement. Only the addition of grazed stratum bulk density to the regression of bite weight on surface height was significant, increasing the proportion of variance accounted for from 0.78 (Equation (5)) to 0.85 (Equation (6)). There was no further improvement from including the interaction term, indicating that surface height and grazed stratum bulk density each had an independent effect on bite weight.

Similarly, for bite weight over the fourteen swards the simple linear regression (Equation (7)) was significantly improved by including a term for surface height in addition to grazed stratum bulk density (Equation (8)). This increased the proportion of variance accounted for from 0.52 to 0.74. Again, the interaction term was not significant.

A comparison of Equations (6) and (8) indicated that neither the intercept nor the slopes of the x-terms were significantly different in

Figure E2.4

The relationship between bite depth and sward surface height, over all seventeen swards

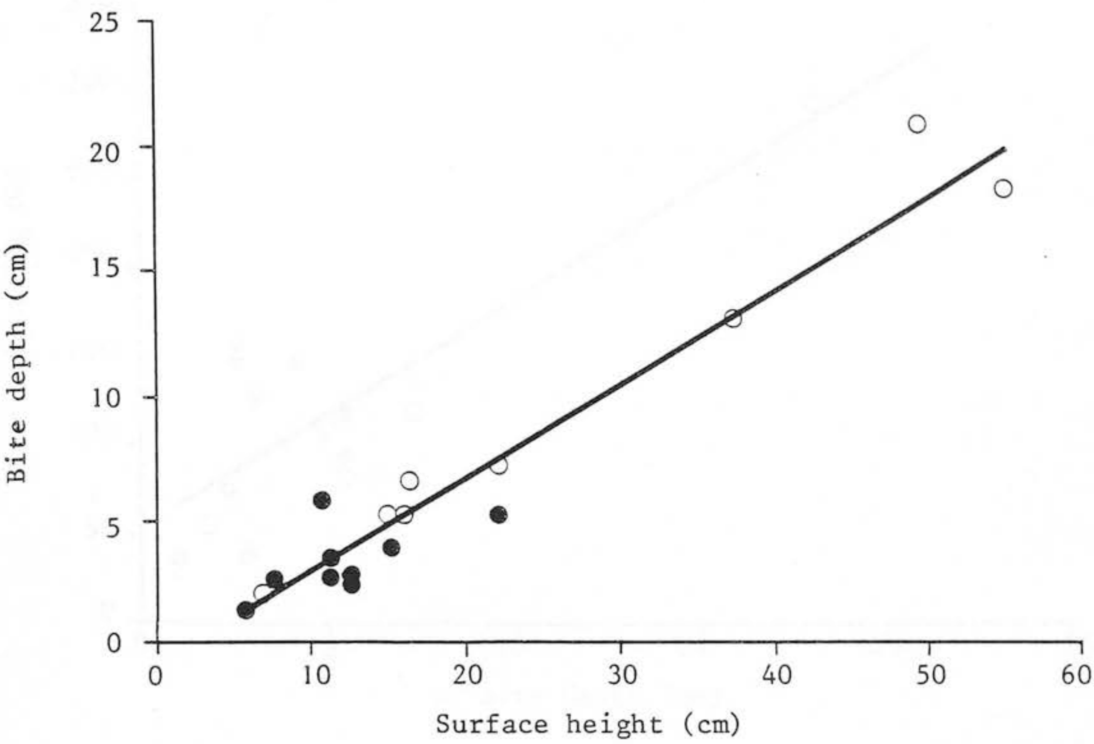


Figure E2.5

The relationship between bite volume and sward surface height, over all seventeen swards

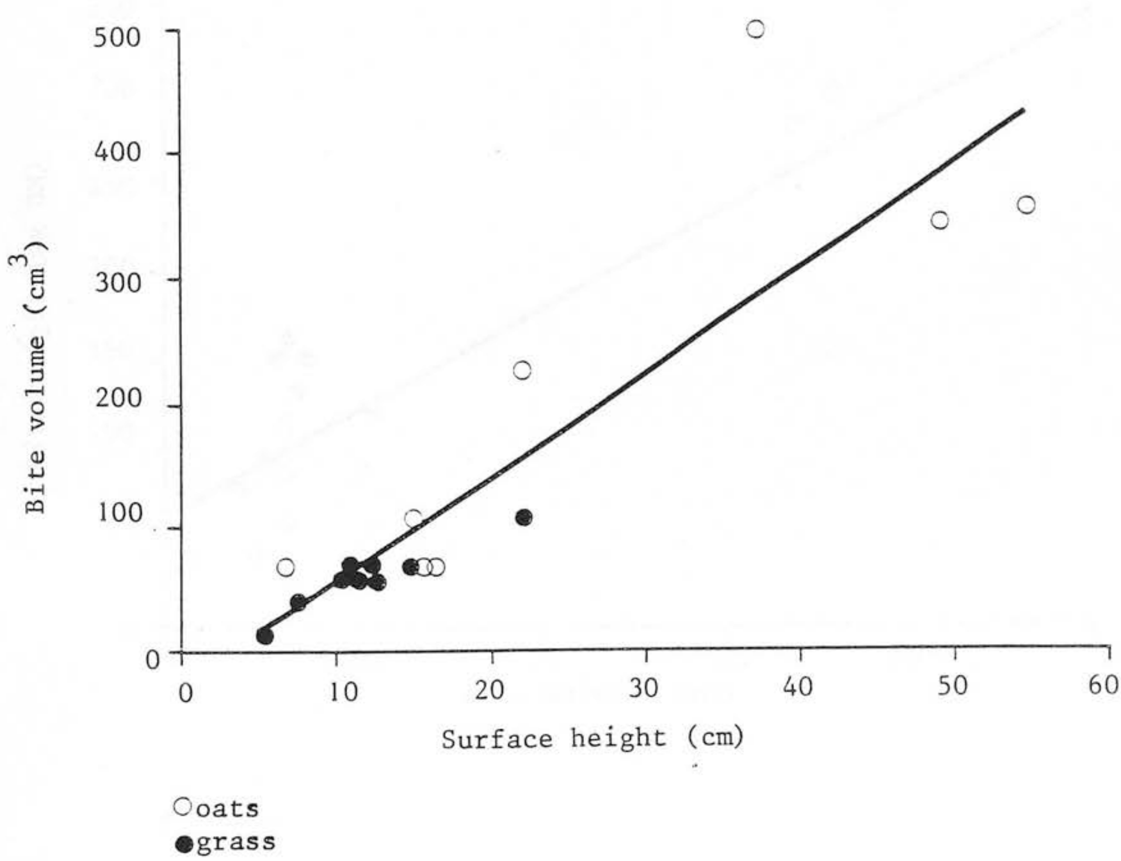


Figure E2.6

The relationship between bite weight and bite depth, over all seventeen swards

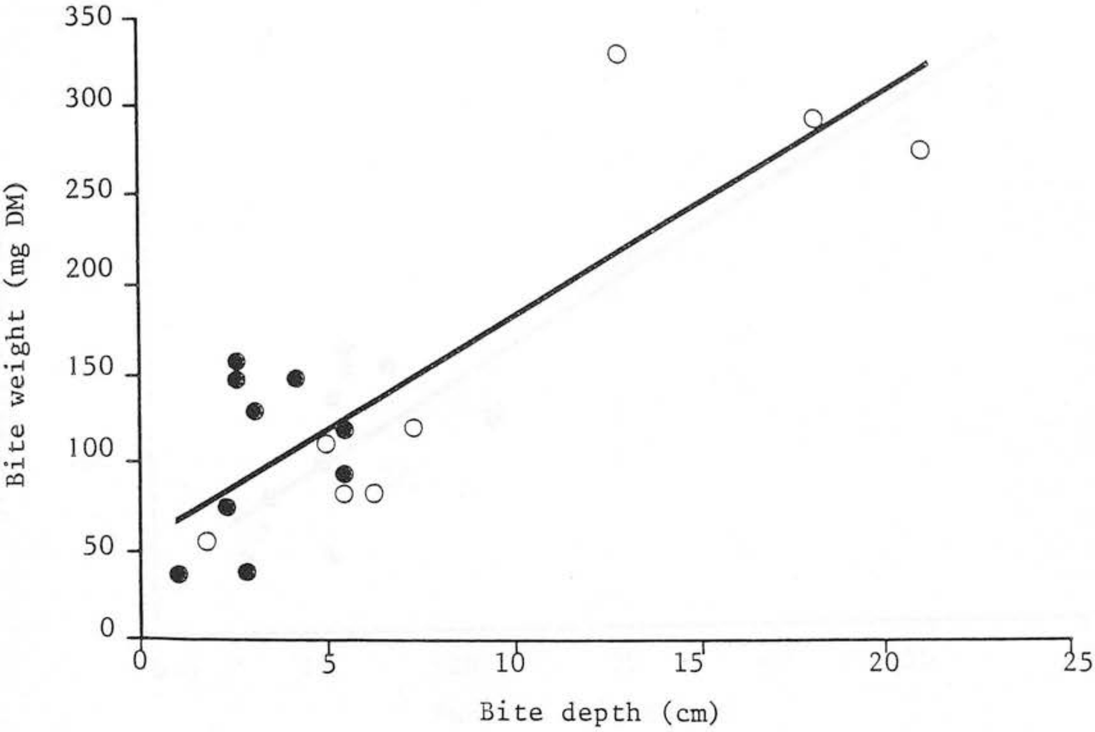


Figure E2.7

The relationship between bite weight and bite volume, over all seventeen swards

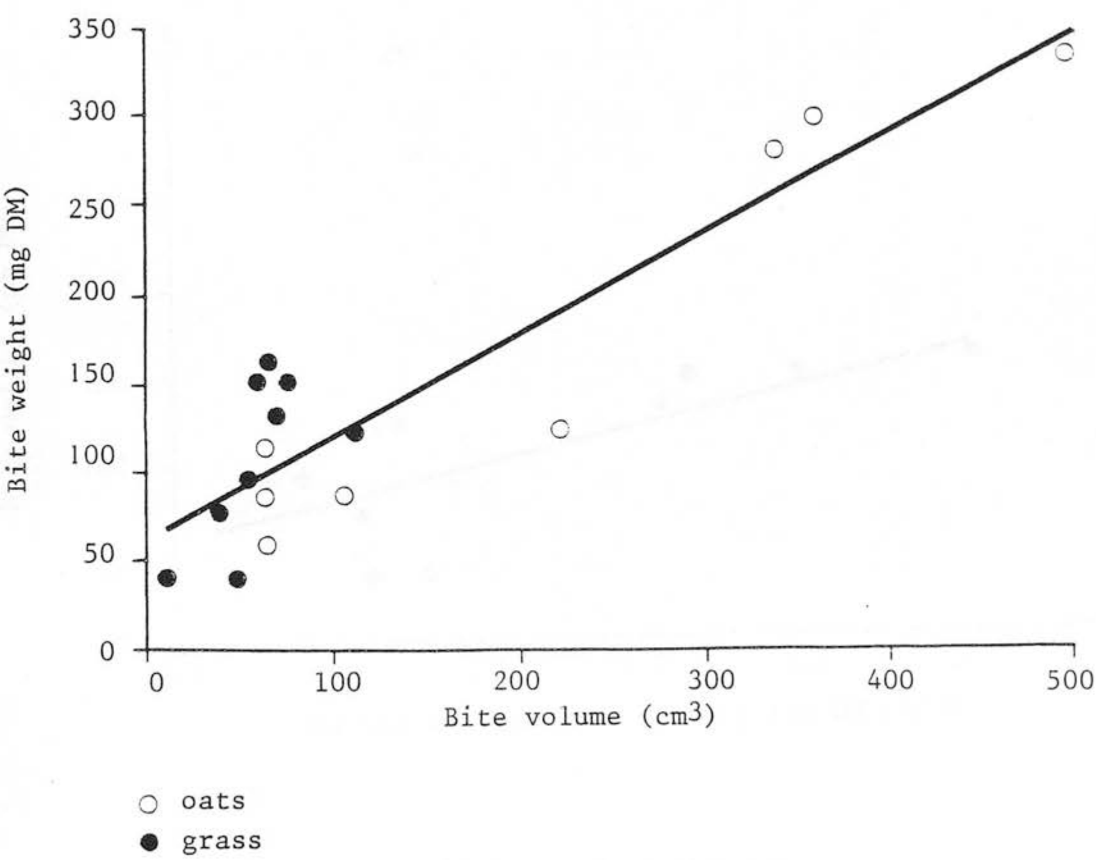


Figure E2.8

The relationship between bite weight and sward surface height, over all seventeen swards

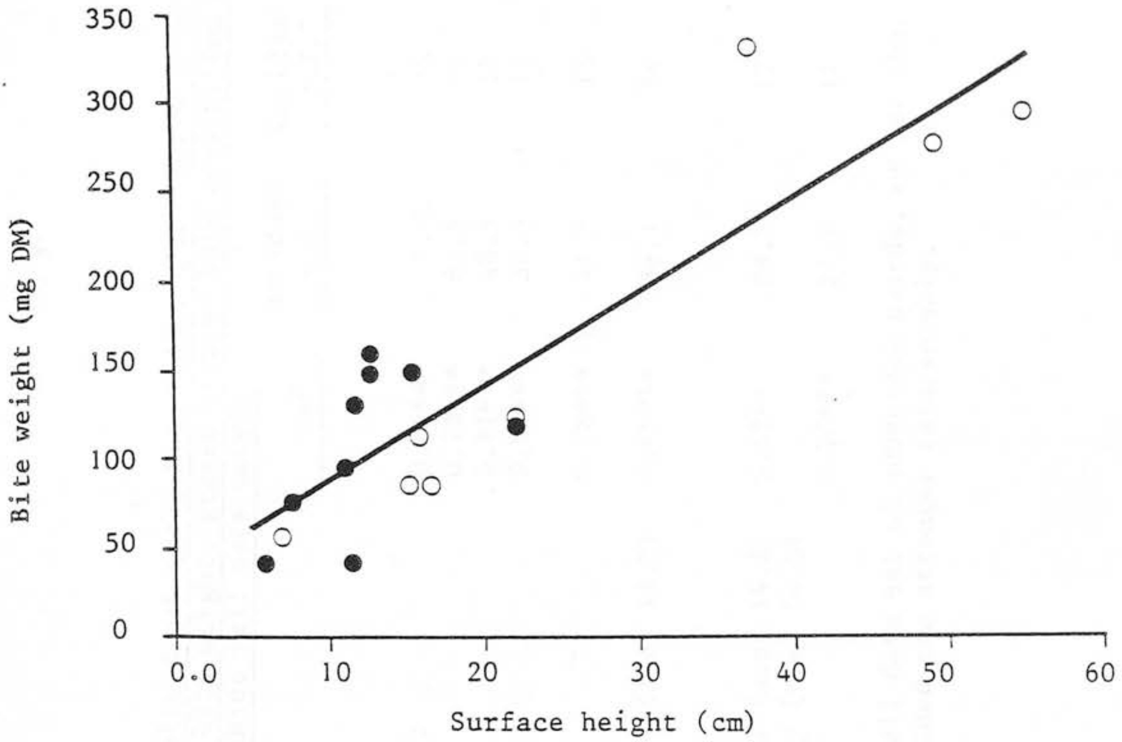
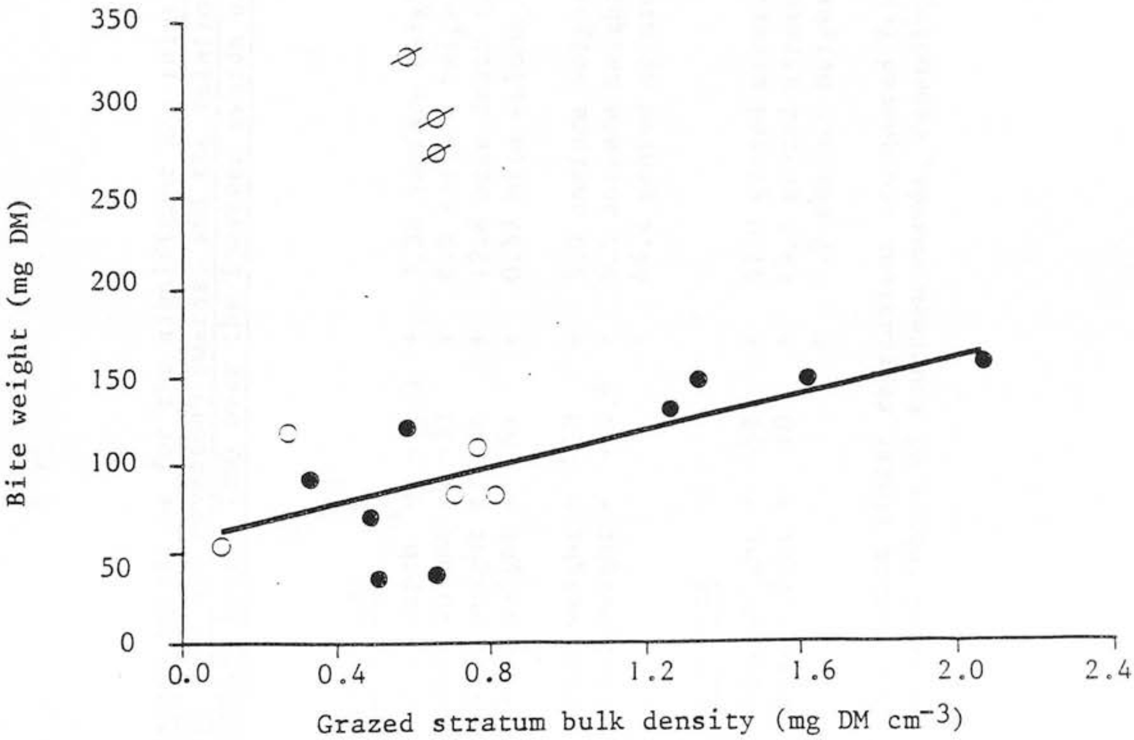


Figure E2.9

The relationship between bite weight and grazed stratum bulk density, over the fourteen swards excluding the three tall oats swards



○ oats

● grass

⌀ tall oats, not included in regression

Table E2.6

Regression equations for the significant key relationships for bite depth (cm), bite volume (cm^3) and bite weight (mg DM) over all seventeen swards, and the relationship between bite weight, grazed stratum bulk density (mg DM cm^{-3}) and surface height (cm) over the fourteen swards excluding the three tall oats swards

					r^2	Residual s.d.	Residual d.f.
	17 swards						
(1)	Bite depth =	- 1.0	+	0.38 surface height (s.e. 0.024)	0.94***	1.42	15
(2)	Bite volume =	-33	+	8.5 surface height (s.e. 1.13)	0.79***	65.5	15
(3)	Bite weight =	54	+	12.8 bite depth (s.e. 2.14)	0.71***	48.5	15
(4)	Bite weight =	61	+	0.57 bite volume (s.e. 0.069)	0.82***	38.3	15
(5)	Bite weight =	33	+	5.3 surface height (s.e. 0.72)	0.78***	41.7	15
(6)	Bite weight =	- 4.9	+	5.5 surface height (s.e. 0.63)			
			+	44.2 grazed stratum bulk density (s.e. 17.9)	0.85***	36.1	14
	14 swards						
(7)	Bite weight =	58	+	51.0 grazed stratum bulk density (s.e. 14.2)	0.52**	28.5	12
(8)	Bite weight =	10	+	49.1 grazed stratum bulk density (s.e. 10.8)			
			+	3.7 surface height (s.e. 1.20)	0.74***	21.7	11

Note: The simple linear regressions are quoted for either the full data set of seventeen swards, or for the reduced subset of fourteen swards, depending on which yielded the stronger relationship.

the seventeen-sward and fourteen-sward situation. It was concluded that the three tall oats swards formed part of the same response continuum as the fourteen shorter swards.

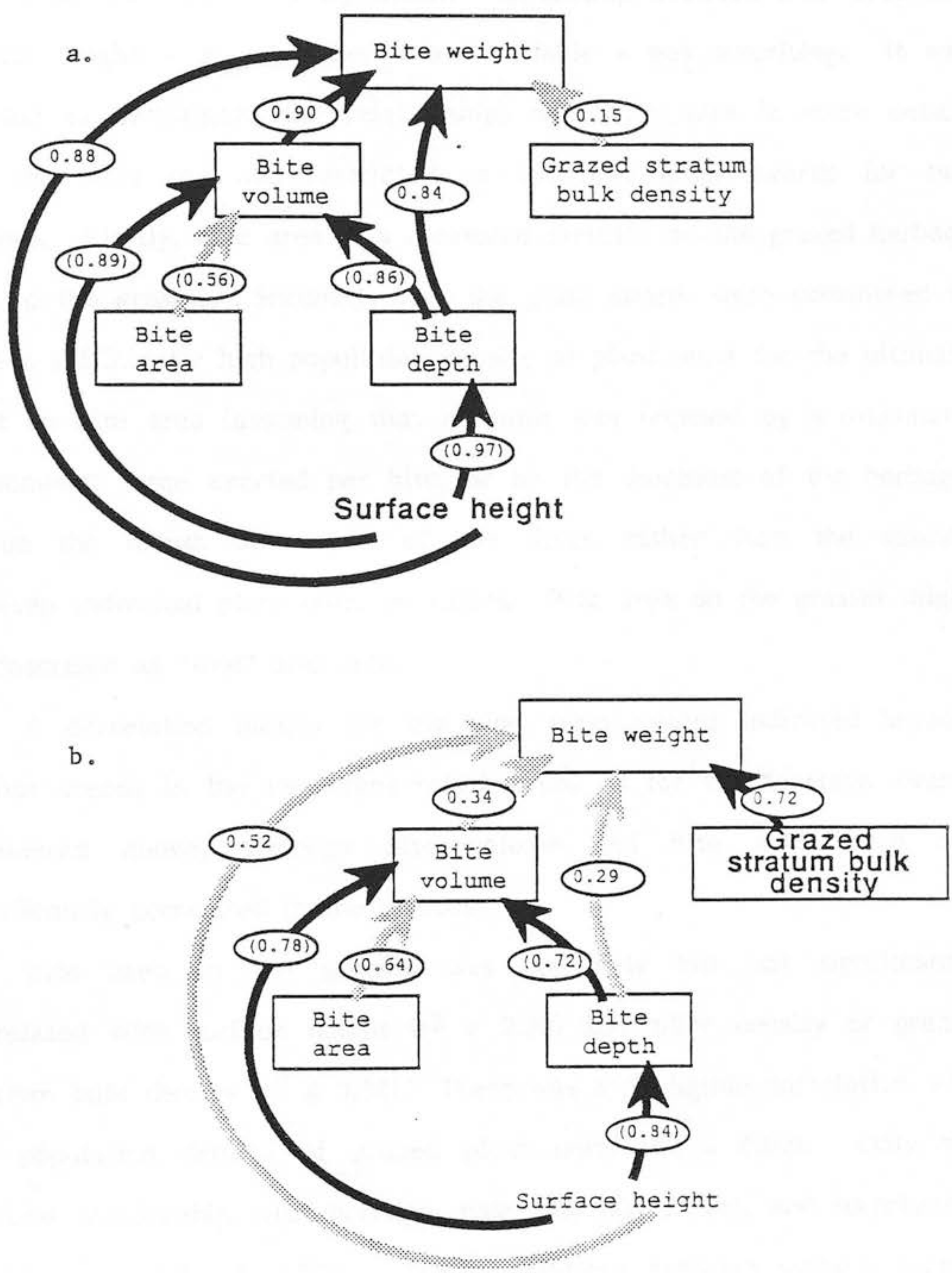
Figure E2.10 illustrates the strength of the interrelationships between bite weight, the bite dimensions, surface height and the grazed stratum bulk density, over all seventeen swards and over the fourteen swards. In both cases, the range in the grazed stratum bulk density was almost twenty-fold, whilst surface height ranged almost ten-fold over the seventeen swards (diagram a.) but less than four-fold over the fourteen swards (diagram b.). This clearly resulted in a switch in the relative importance of surface height and grazed stratum bulk density in influencing bite weight, the former having the greater impact over all seventeen swards and the latter over the fourteen swards with a limited height range.

The effect of surface height on bite weight was evidently mediated via bite depth and volume. In both situations, there was a strong correlation between surface height and bite depth, but a slightly weaker correlation between surface height and bite volume due to the "diluting" effect of bite area which did not appear to be strongly related to surface height, or indeed to any other sward variable. Bite volume then had a strong influence on bite weight in the seventeen-sward situation, but a much weaker effect over the fourteen swards with a limited height range.

As a comparison with Experiment 1, the most comprehensive regressions relating a) bite depth and b) bite weight to sward variables over all seventeen swards (Equations (1) and (6) in Table 2.6 respectively) were tested for the addition of a term for the five different crops used. In neither case was there a significant "crop" effect.

Figure E2.10

Diagrams showing the correlation coefficients for the relationships between bite weight, the bite dimensions, surface height and grazed stratum bulk density, over a. all seventeen swards and b. fourteen swards, excluding the three tall oats swards



Notes: Correlation coefficients in parentheses denote relationships between variables which were not measured independently.
Pale arrows indicate relationships which are either not significant or significant at $P<0.05$.
Dark arrows indicate relationships significant at $P<0.01$ or $P<0.001$.

Bite area and the theory of a summit force per bite

In view of the strong influence of sward surface height on both bite depth and bite volume in the seventeen-sward and fourteen-sward data sets, the lack of a significant relationship between bite area and surface height - or any other sward variable - was surprising. It was decided to investigate the relationships with bite area in more detail, and the data set was restricted to the nine grass swards for two reasons. Firstly, bite area was measured directly on the grazed herbage only in the grasses. Secondly, only the grass swards were considered to have a sufficiently high population density of plant units for the ultimate limit on bite area (assuming that no limit was imposed by a maximum, or summit, force exerted per bite, or by the shortness of the herbage) to be the mouth dimensions of the sheep rather than the spacing between individual plant units or tillers. Bite area on the grasses might be described as "true" bite area.

A correlation matrix for the nine grass swards indicated broadly similar trends in the important relationships as for the fourteen swards considered above, although bite volume and bite area were not significantly correlated in the grasses.

Bite area in the grasses was positively but not significantly correlated with surface height (r^2 = 0.20) and tiller density or grazed stratum bulk density ($r^2 \leqslant 0.38$). There was a negligible correlation with the population density of grazed plant units (r^2 = 0.02). Only the positive relationship with herbage mass was significant, and surprisingly strong (r^2 = 0.81, $P<0.001$). The correlations between surface height, herbage mass, bite depth, bite area and bite volume are presented in Table E2.7.

The regression for the relationship between bite area (cm^2) and herbage mass (kg DM ha^{-1}) was found not to deviate significantly from

Table E2.7

Correlation matrix for the key relationships for the nine grass swards

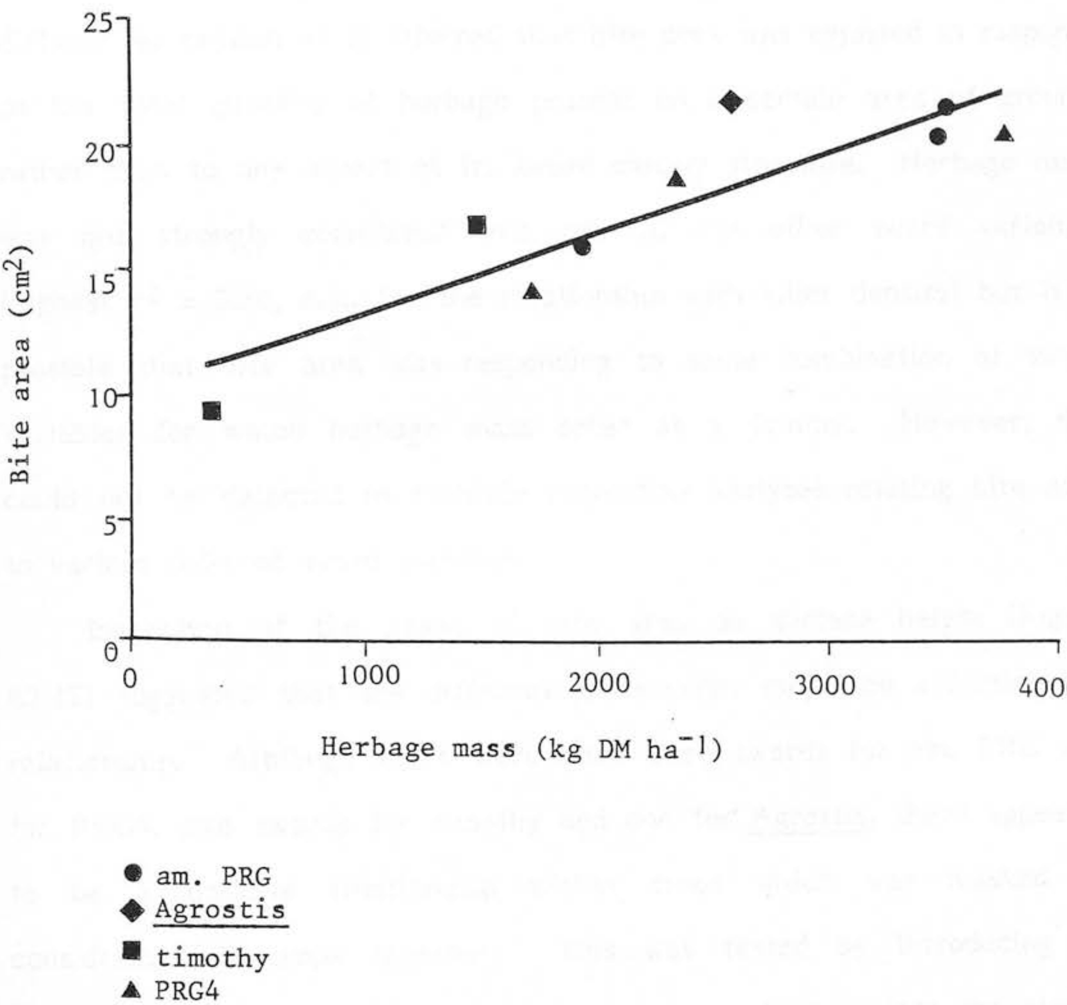
d.f. = 7

herbage mass	0.49			
bite depth	(0.71*)	-0.11		
bite area	0.45	0.90***	-0.20	
bite volume	(0.96***)	0.50	(0.76*)	(0.47)
	surface height	herbage mass	bite depth	bite area

Notes: Correlation coefficients in parentheses denote relationships between variables which were not measured independently.
Correlation coefficients for which the level of statistical significance is not indicated are not significant ($P \geqslant 0.05$).

Figure E2.11

The relationship between bite area and herbage mass, over the nine grass swards



linearity and the regression line is illustrated in Figure E2.11. The equation was:

Bite area = 9.8 + 0.0033 herbage mass (s.e. 0.00060);

r^2 = 0.81***, residual s.d. = 1.93, residual d.f. = 7.

The strong relationship between bite area and herbage mass was difficult to explain as it inferred that bite area was adjusted in response to the total quantity of herbage present on a certain area of ground, rather than to any aspect of its sward canopy structure. Herbage mass was not strongly correlated with any of the other sward variables (highest r^2 = 0.36, n.s., for the relationship with tiller density) but it is possible that bite area was responding to some combination of sward variables for which herbage mass acted as a dummy. However, this could not be detected in multiple regression analyses relating bite area to various pairs of sward variables.

Inspection of the graph of bite area on surface height (Figure E2.12) suggested that the different grass crops might be affecting the relationship. Although there were only three swards for am. PRG and for PRG4, two swards for timothy and one for Agrostis, there appeared to be a positive relationship within crops which was masked by considering all crops together. This was tested by introducing an additional term for individual crops or groups of crops into the simple linear regression of bite area on surface height. There was a significant improvement when the term "crop groups" (either the two timothy swards or the seven other grass swards) was fitted to give parallel lines:

$$\left.\begin{array}{ll}\text{Bite area (timothy)} & = 7.2 \\ & \\ \text{Bite area (all other grasses)} & = 13.5\end{array}\right\} + 0.45 \text{ surface height (s.e. 0.213);}$$

r^2 = 0.65*, residual s.d. = 2.80, residual d.f. = 6

These regression lines are illustrated in Figure E2.12.

Figure E2.12

The relationship between bite area and sward surface height, over the nine grass swards

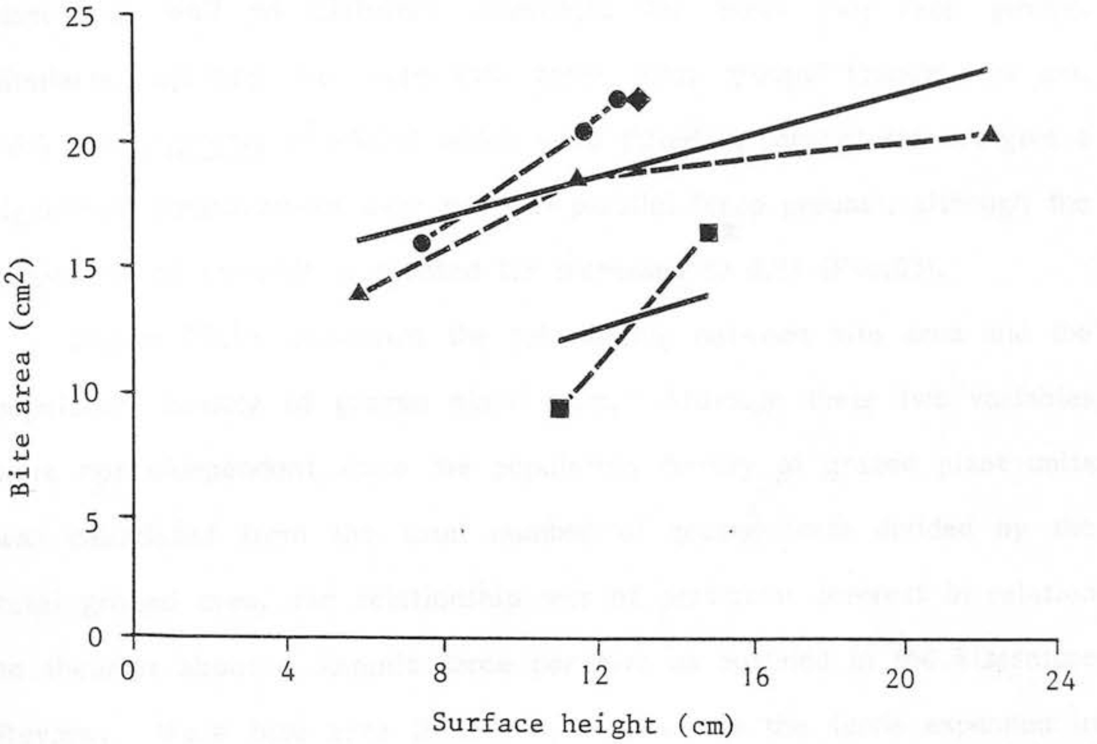
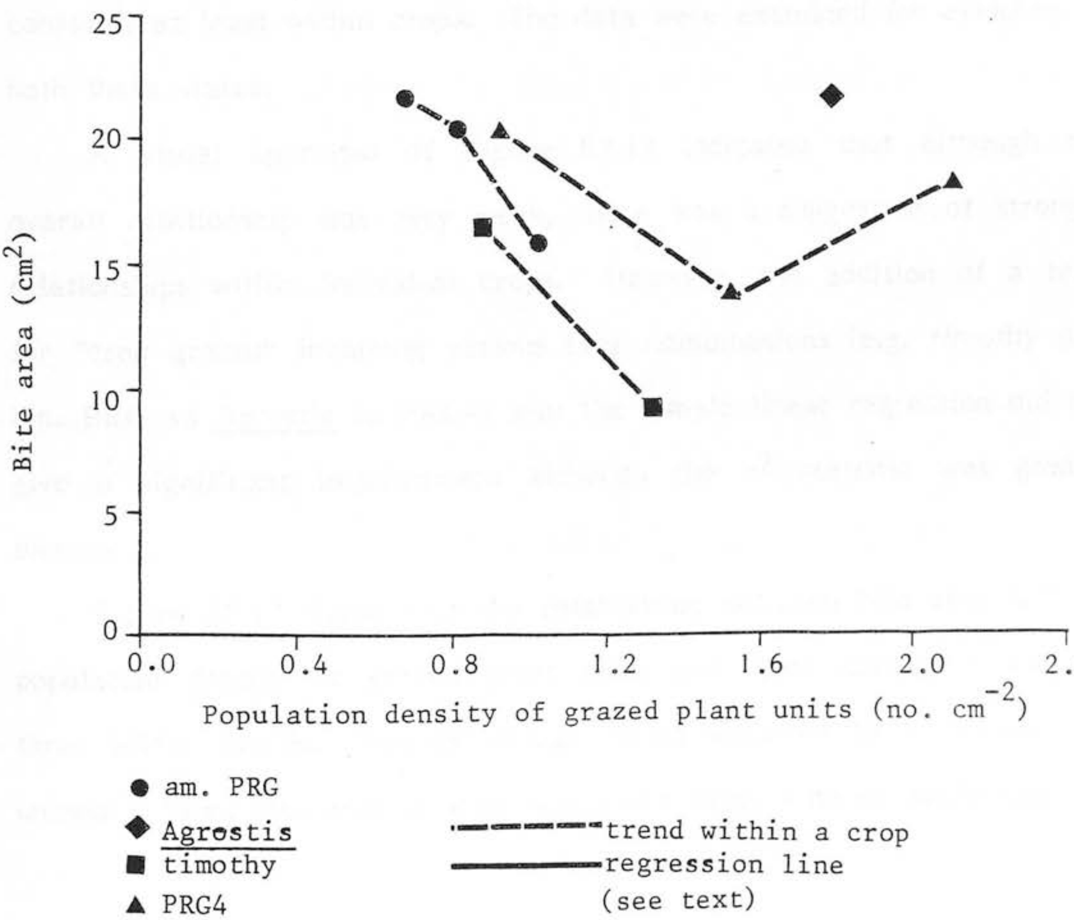


Figure E2.13

The relationship between bite area and the population density of grazed plant units, over the nine grass swards



There was no further significant improvement by fitting different slopes as well as different intercepts for these two crop groups. Similarly, splitting the crops into three "crop groups" (timothy vs am. PRG plus Agrostis vs PRG4) which were fitted in parallel did not give a significant improvement over the two parallel "crop groups", although the proportion of variance accounted for increased to 0.81 ($P<0.05$).

Figure E2.13 illustrates the relationship between bite area and the population density of grazed plant units. Although these two variables were not independent since the population density of grazed plant units was calculated from the total number of grazed units divided by the total grazed area, the relationship was of particular interest in relation to theories about a summit force per bite as outlined in the Literature Review. Were bite area limited by a limit to the force expended in harvesting a bite, it would be expected that, firstly, bite area would be negatively related to the population density of grazed plant units, and secondly the number of grazed plant units per bite would be reasonably constant, at least within crops. The data were examined for evidence of both these states.

A visual appraisal of Figure E2.13 indicated that although the overall relationship was very weak, there was a suggestion of stronger relationships within individual crops. However, the addition of a term for "crop groups" involving various crop combinations (e.g. timothy plus am. PRG vs Agrostis vs PRG4) into the simple linear regression did not give a significant improvement although the r^2 statistic was greatly increased.

Figure E2.13 shows that the relationship between bite area and the population density of grazed plant units was least consistent for the three PRG4 swards. The PRG4 LgP sward appeared to have either an unusually large bite area or - perhaps more likely - an unusually high population density of grazed plant units. This sward, unlike the other grass swards, was pre-cut only five days before sampling and it is possible that some cut units were wrongly assessed as having been grazed. This would result in overestimates of both the number of grazed plant units per bite and the population density of grazed plant units, provided that there was no corresponding overestimate of bite area.

Data for the mean number of grazed plant units per bite on each of the grass swards are presented in Table E2.8. If it is assumed that sheep did not take successive bites on the same plant units, then on average the animals severed between 12 and 38 plant units at a bite. Whilst the between-sward differences were highly significant ($P<0.001$), there were no significant differences between individual sheep. Within crops, the three am. PRG swards did not differ significantly, nor did the two timothy swards, but the number of grazed plant units per bite was significantly higher (approximately double) on the PRG4 LgP sward than on the LgG or SG swards. In order for the three PRG4 swards not to have differed significantly, the value for LgP would have had to have been at least 37% less, and it is questionable whether the count of grazed plant units was overestimated by the inclusion of cut plant units to such an extent.

If there were large differences between swards within crops in the proportion of stems in the grazed plant units, then any test of the hypothesis of a summit force per bite would have to take into account both the likely differences in the tensile properties of leaves and stems, and the relative proportions of leaves and stems severed. Table E2.8 shows that over all swards the mean proportion of stems in the grazed plant units did not exceed 0.12 and was usually considerably less than this. The proportion of stems in the grazed plant units did not differ

Table E2.8

The number of grazed plant units per bite and the proportion of stems in the grazed plant units, on the grass swards

Trial and month	Crop	Sward	Number of grazed plant units per bite	Proportion of stems in grazed plant units
2 Aug.	am. PRG	H	16.1^{abc}	$<0.01^{a}$
		M	14.5^{ab}	$<0.001^{a}$
		HC	15.4^{ab}	0.05^{b}
3 Sept.	*Agrostis* timothy	L	38.3^{d}	0.06^{bc}
		HG	12.0^{a}	0.12^{c}
		HC	13.9^{ab}	0.07^{bc}
4 Oct.	PRG4	LgP	35.7^{d}	$<0.01^{a}$
		LgG	17.9^{bc}	$<0.01^{a}$
		SG	20.4^{c}	0.01^{a}
s.e. of sward means			1.60	0.019
significance of differences				
between swards			***	***
between sheep			n.s.	n.s.

Notes: Sward means with different superscripts are significantly different ($P<0.05$).
The s.e. of sward means presented is an average value; when there are large differences in the size of table entries it may not be appropriate to each entry.

significantly between the PRG4 swards or between the timothy swards but it did between the am. PRG swards.

To summarise the results of the examination of bite area within the grasses, it would appear that bite area was related to herbage mass, surface height and the population density of grazed plant units, although crop effects were apparently confounded with the last two variables. Whilst in general the data would appear to be in accord with the theory of a summit force per bite, the measurements on the PRG4 LgP sward were contradictory, and it must be concluded that there was insufficient evidence from this experiment to either confirm or refute the theory.

Diet selection

For the purposes of examining diet selection within the cage patches, the sward was considered to comprise only two components : leaf (lamina) and stem (pseudostem, flowering stem and flowerhead).

Three different aspects of potential diet selection were investigated. Two mechanisms were proposed whereby the sheep might preferentially remove either leaf or stem from a sward with both of these components in the surface stratum, and the hypotheses were tested on the oats swards. As these mechanisms would, in theory, operate predominantly in different planes, they were termed horizontal selection and vertical selection respectively. The third aspect of diet selection to be investigated was whether or not grazing was confined to the leafy surface stratum in the vegetative (grass) swards, with the stratum containing pseudostem acting as a barrier to deeper grazing. Possible sward characteristics limiting bite depth in the oats swards were also considered briefly.

Horizontal selection

In any sward with a heterogenous surface stratum, it is possible that selection of leaf or stem might be effected by the sheep selecting, from above, areas of sward or particular tillers with a relatively large amount of the preferred component. Indeed the sheep might select individual leaves or stems, but of course the structure of the gramineous plant does not facilitate the grazing of stems without the associated leaves, unless flower and flowering stem above the flag leaf are selected.

This hypothesis of horizontal selection was tested by comparing the proportion of leaves in the grazed plant units with the corresponding proportion of leaves in the cut plant units. It was assumed that these two proportions would not differ significantly if the sheep were not selecting between leaf and stem in a horizontal plane. The hypothesis could only be tested on the oats swards as only these had some stem in addition to leaf in the surface stratum.

Table E2.9 shows the mean sward values for the proportion of leaves in the grazed plants units (range 0.3 - 0.6; significant differences between swards, $P<0.01$, and between individual sheep, $P<0.05$) and the proportion of leaves in the cut plant units (range 0.6 - 0.9; significant differences between swards, $P<0.001$, but not between sheep). On average over all oats swards, only 0.47 of the grazed plant units were leaves, compared with 0.67 of the cut plant units. Grazing resulted in a significantly lower proportion of leaves in the severed units on all swards except oats MP where a similar proportion was both cut and grazed. This surprising result indicated that on the oats swards sheep generally selected stem rather than leaf as in most previous work. The greatest selection for stem apparently occurred on the two regrowth swards, MG and HC.

Following Chesson (1978, 1983), leaf selection indices were calculated for each cage patch as follows:

Table E2.9

A comparison of the proportion of leaves in the grazed plant units and in the cut plant units, the resulting leaf selection index, and the number of grazed plant units per bite, on each of the oats swards

Trial, month and crop	Sward	Proportion of leaves in plant units severed by grazing		Proportion of leaves in plant units severed by cutting	Significance of difference between grazing and cutting	Leaf selection index	Number of grazed plant units per bite
1 July/Aug. oats	H	0.39		0.59	**	0.30	1.3
	L	0.42		0.64	**	0.30	1.6
	M	0.41		0.64	**	0.28	1.3
	LP	0.34		0.55	**	0.31	1.2
	MP	0.62		0.60	n.s.	0.51	2.4
	HP	0.48		0.62	*	0.36	2.1
	MG	0.54		0.89	***	0.13	0.9
	HC	0.55		0.82	***	0.22	2.6
s.e. of grazing and cutting means within a sward			0.043				
s.e. of sward means[a]		0.041		0.048		0.053	0.23
significance of differences							
between swards		**		***		**	***
between sheep		*		n.s.		n.s.	n.s.
overall mean		0.47		0.67			
s.e.			0.015				

a The s.e. presented is an average value; when there are large differences in the size of table entries it may not be appropriate to each entry.

$$\text{Leaf selection index} = \frac{\dfrac{\text{p leaves grazed}}{\text{p leaves cut}}}{\dfrac{\text{p leaves grazed}}{\text{p leaves cut}} + \dfrac{\text{p stems grazed}}{\text{p stems cut}}}$$

where p leaves grazed = proportion of leaves in grazed plant units;
p stems cut = proportion of stems in cut plant units, etc.

Possible values for the index range from 0 (total rejection of leaf) through 0.5 (no discrimination between leaf and stem) to 1 (total selection for leaf). The calculated values are presented on a sward mean basis in Table E2.9, and ranged from 0.5 on oats MP to 0.1 on the regrowth MG. There were significant differences between swards ($P<0.01$) but not between sheep.

Table E2.9 also shows the mean number of grazed plant units per bite on each of the oats swards. Values ranged from 0.9 on the regrowth MG to 2.6 on the regrowth HC. There were significant differences between swards ($P<0.001$) but not between sheep. The number of grazed plant units per bite was considerably less on the oats swards than on the grass swards (Table E2.8 ; range 12-38), and this was undoubtedly a reflection of the sparsity of the oats swards compared with the grasses. Just as the number of grazed plant units per bite was examined within the grass swards in relation to the theory of a summit force per bite, this variable was examined within the oats swards in relation to the degree of diet selection exerted by the sheep.

Scatter diagrams and a correlation matrix for the oats swards, based on the variables presented in Table 2.9 in addition to the sward and bite variables used in previous matrices, were used to investigate which sward variables might have influenced selection and what effect, if any, selection had on the various bite measurements.

The correlation matrix indicated broadly similar trends in the important relationships with the bite measurements for the eight oats swards as compared with all seventeen swards. The key relationships within the oats swards involving measures of diet selection are presented in Table E2.10.

The proportion of leaves in the grazed plant units was not significantly related to any sward variable, although as might be expected this proportion was positively correlated with the corresponding proportion in the cut plant units. Whilst the leaf selection index was positively but only weakly related to the proportion of leaves in the grazed plant units, the relationship with the corresponding proportion in the cut plant units was negative and statistically significant ($P<0.05$). This suggested that sheep tended to become more selective, grazing stem in preference to leaf, as the proportion of leaves in the sward at the mean grazed height increased (Figure E2.14). However, it must be borne in mind that the leaf selection index was derived from estimates of the proportion of leaves in both the grazed and the cut plant units and was therefore not independent of these proportions.

The leaf selection index was also significantly positively correlated with the grazed stratum bulk density (Table E2.10; Figure E2.15) although this might have been due to the strong negative relationship between the grazed stratum bulk density and the proportion of leaves in the cut plant units. In addition, the leaf selection index was positively related to the population density of grazed plant units but the correlation failed to reach the 0.05 significance level (Table E2.10). Sheep might have selected stem to an increasing extent because the declining sward density allowed a greater degree of discrimination, or simply because the stem component was scarcer in the sward and therefore considered more desirable. The appeal of grazing the heavier component, stem, might also have been enhanced as the sward became sparser because it would be increasingly difficult to harvest a heavy bite.

Table E2.10

Correlation matrix for the key relationships with the proportion of leaves in the grazed plant units and the leaf selection index, over the eight oats swards

	leaf selection index	proportion of leaves in grazed plant units	proportion of leaves in cut plant units	grazed stratum bulk density	population density of grazed plant units
proportion of leaves in grazed plant units	(0.19)			d.f. = 6	
proportion of leaves in cut plant units	(−0.73*)	0.53			
grazed stratum bulk density	0.75*	−0.47	−0.98***		
population density of grazed plant units	0.64	0.13	−0.48	0.61	
number of grazed plant units per bite	0.54	0.64	−0.02	0.09	0.47

Notes: Correlation coefficients in parentheses denote relationships between variables which were not measured independently.
Correlation coefficients for which the level of statistical significance is not indicated are not significant ($P \geqslant 0.05$).

Figure E2.14

The relationship between the leaf selection index and the proportion of leaves in the cut plant units, over the eight oats swards

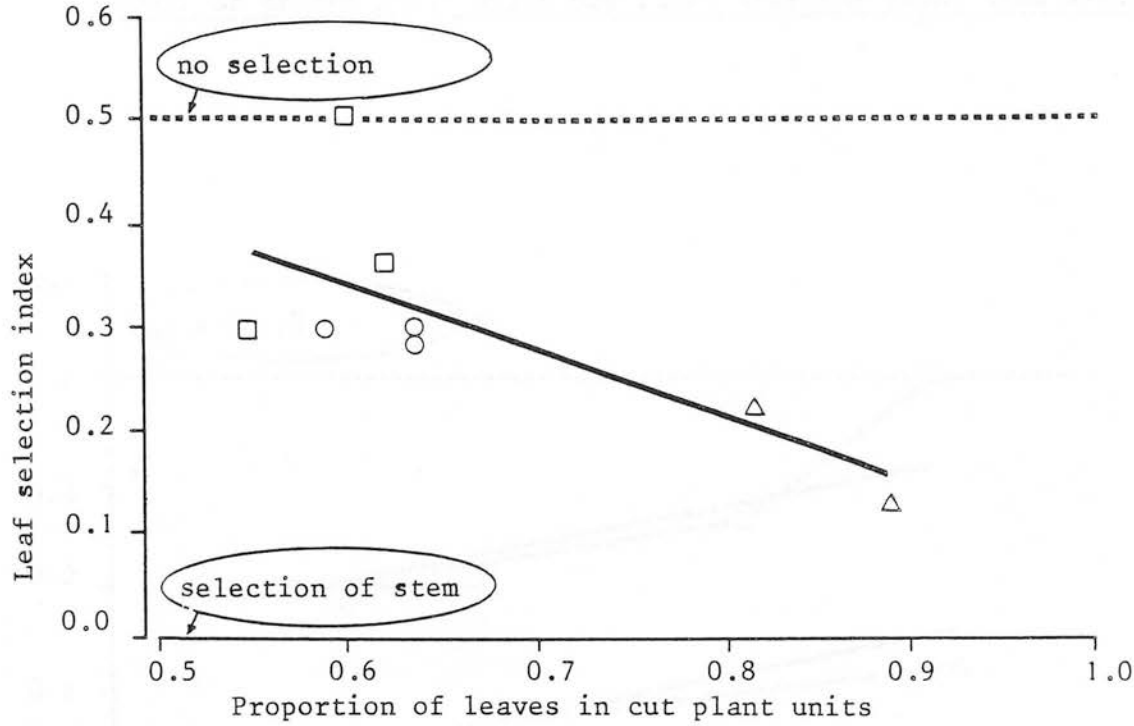
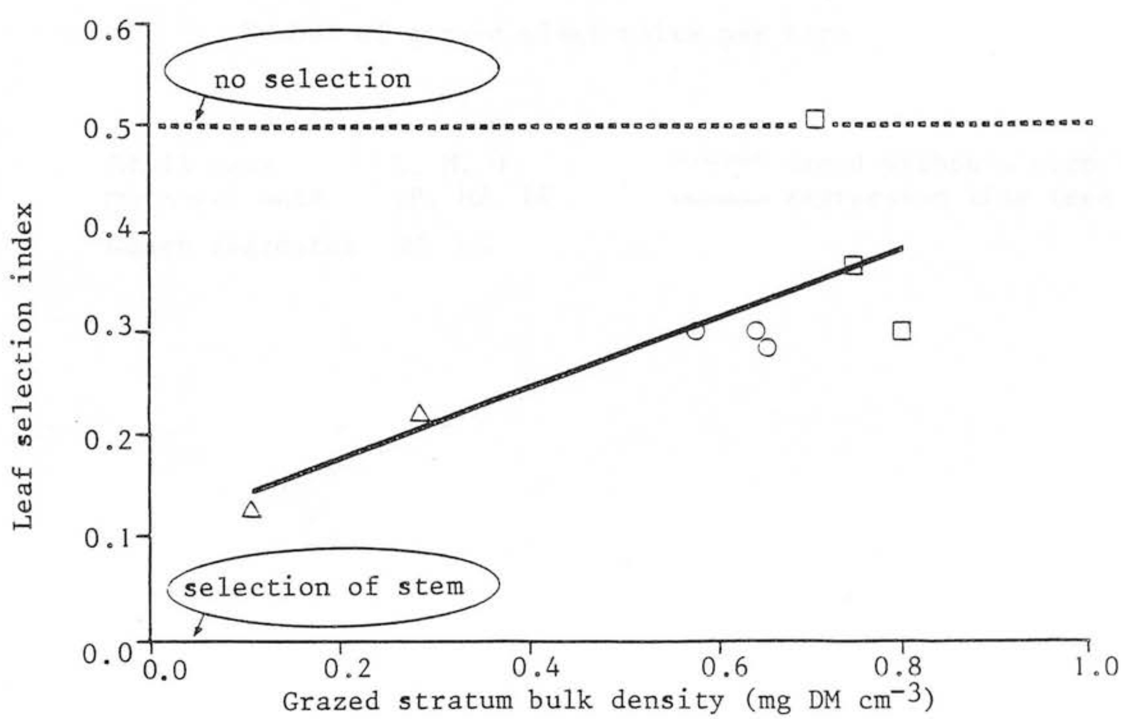


Figure E2.15

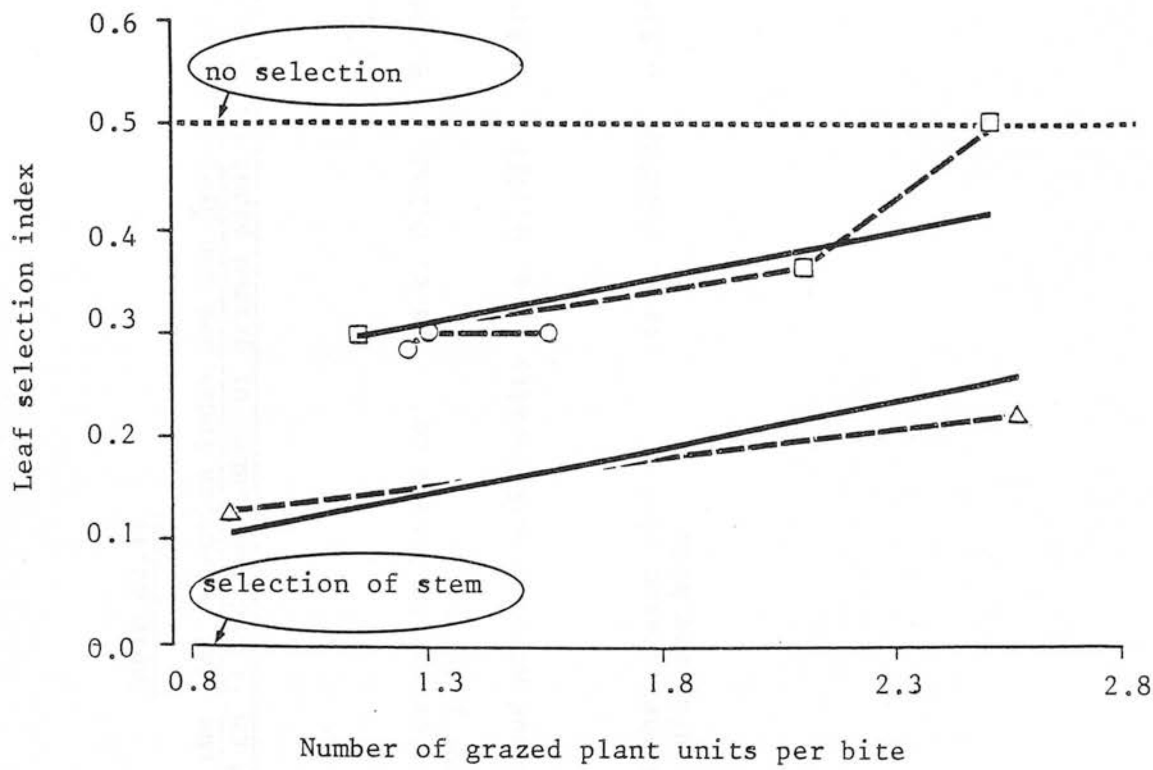
The relationship between the leaf selection index and the grazed stratum bulk density, over the eight oats swards



○ tall oats L, M, H
□ pre-cut oats LP, MP, HP
△ oats regrowths MG, HC

Figure E2.16

The relationship between the leaf selection index and the number of grazed plant units per bite, over the eight oats swards



○ tall oats L, M, H — trend within a crop

□ pre-cut oats LP, MP, HP — regression line (see text)

△ oats regrowths MG, HC

Table E2.11

Regression equations for the relationships between the leaf selection index and the proportion of leaves in the cut plant units, the grazed stratum bulk density (mg DM cm^{-3}) and the number of grazed plant units per bite, over the eight oats swards

						r^2	Residual s.d.	Residual d.f.
Leaf selection index	=	0.74	-	0.65 proportion of leaves in cut plant units	(s.e. 0.250)	0.53*	0.080	6
Leaf selection index	=	0.11	+	0.33 grazed stratum bulk density	(s.e. 0.118)	0.57*	0.076	6
Leaf selection index (oats regrowths)	=	0.0063	+	0.099 number grazed plant units per bite	(s.e. 0.0293)	0.85**	0.050	5
Leaf selection index (all other oats swards)	=	0.18						

The impact of diet selection on bite dimensions and bite weight appeared to be minor. Correlations between either the proportion of leaves in the grazed plant units or the leaf selection index, and bite depth, area, volume and weight were low ($r^2 \leqslant 0.32$, n.s.) and might have resulted from confounding with other variables. Furthermore, for the oats data set none of the key regressions of bite depth, volume or weight on sward surface height ($r^2 = 0.95$, $P<0.001$; $r^2 = 0.70$, $P<0.001$; and $r^2 = 0.85$, $P<0.01$ respectively) was significantly improved by the addition of a term for the leaf selection index.

Although the positive relationship between the leaf selection index and number of grazed plant units per bite was not significant over all eight oats swards (Table E2.10), the relevant graph indicated a stronger relationship within each of the three types of oats swards; tall, pre-cut and regrowth (Figure E2.16). When an x-term for the two-level factor "sward age" (the tall primary swards plus the freshly cut swards vs the two regrowth swards) was added to the simple linear regression of leaf selection index on number of grazed plant units per bite, the relationship became significant ($P<0.01$) and the proportion of variance accounted for increased from 0.30 to 0.85. There was no further significant improvement by fitting separate slopes for the two lines, or by fitting three parallel lines - one for each of the sward types.

The reason for selection of stem being greater on the regrowth was probably the lower proportion of stems in the cut plants units, or the lower grazed stratum bulk density of these swards.

The equations for the regressions of the leaf selection index on the proportion of leaves in the cut plant units, the grazed stratum bulk density and the number of grazed plant units per bite, illustrated in Figures E2.14, E2.15 and E2.16 respectively, are given in Table E2.11. Tests on the first two regressions indicated that these did not deviate significantly from linearity, nor were they improved significantly by adding a term for surface height, herbage mass, tiller density or the density of the grazed plant units. Neither regression was improved upon by the inclusion of the x-terms from both regressions in a multiple regression.

Vertical selection

It was postulated that, following any selection for stem in a horizontal plane on swards with a heterogenous surface stratum, the sheep might preferentially graze a particular sward component in a vertical plane. Although it is easy to envisage the sheep stripping leaves off the predominantly reproductive and relatively sparsely spaced oats stems, any vertical selection for stem would presumably be limited by the practical difficulties in grazing stem without leaf.

In order to test the hypothesis of vertical selection in the oats swards, a comparison was drawn between the mean grazed height of leaves and of stems. If either component was preferentially grazed then it was suggested that this would be reflected in a lower grazed height.

The results are shown in Table E2.12. The mean of the grazed leaf height and grazed stem height differed significantly between swards ($P<0.001$), but within swards leaf was not consistently grazed to a greater or lesser height than stem. Differences between the mean grazed heights of the two components ranged from 0.2 to 2.4 cm and were not significant. It was concluded that there was no evidence of selection for either stem of leaf in a vertical plane in the oats swards.

Influence of pseudostem

Swards with a homogenous (leafy) surface stratum do not present the same opportunities for horizontal and vertical selection as described above. Until the leafy stratum has been removed and the pseudostem exposed there is no real choice available between leaf and pseudostem.

Table E2.12

A comparison of the mean grazed height of leaf and stem on each of the oats swards

Trial, month and crop	Sward	Mean of grazed leaf height and grazed stem height (cm)	Difference between mean grazed leaf height and mean grazed stem height (cm)
1	H	36.8	-1.24
July/Aug.	L	24.4	-2.43
oats	M	28.0	-0.26
	LP	10.7	2.38
	MP	9.3	0.27
	HP	10.8	-0.74
	MG	5.7	0.71
	HC	14.8	-0.15
s.e.d. within swards[a]			0.96
s.e. of sward means[a]		1.53	
significance of differences			
within swards			n.s.
between swards		***	

a The s.e.d. and s.e. presented are average values; when there are large differences in the size of table entries they may not be appropriate to each entry.

Even in a sward with exposed pseudostem, preferential grazing would be comparatively difficult to implement. The sheep would have to be very sensitive to the difference between pseudostem and leaf, and in order to select leaf would have to be sufficiently dextrous to remove this component without pseudostem. This would, presumably, be increasingly difficult in denser swards. The preferential removal of pseudostem from the sward would be very difficult and appears most unlikely.

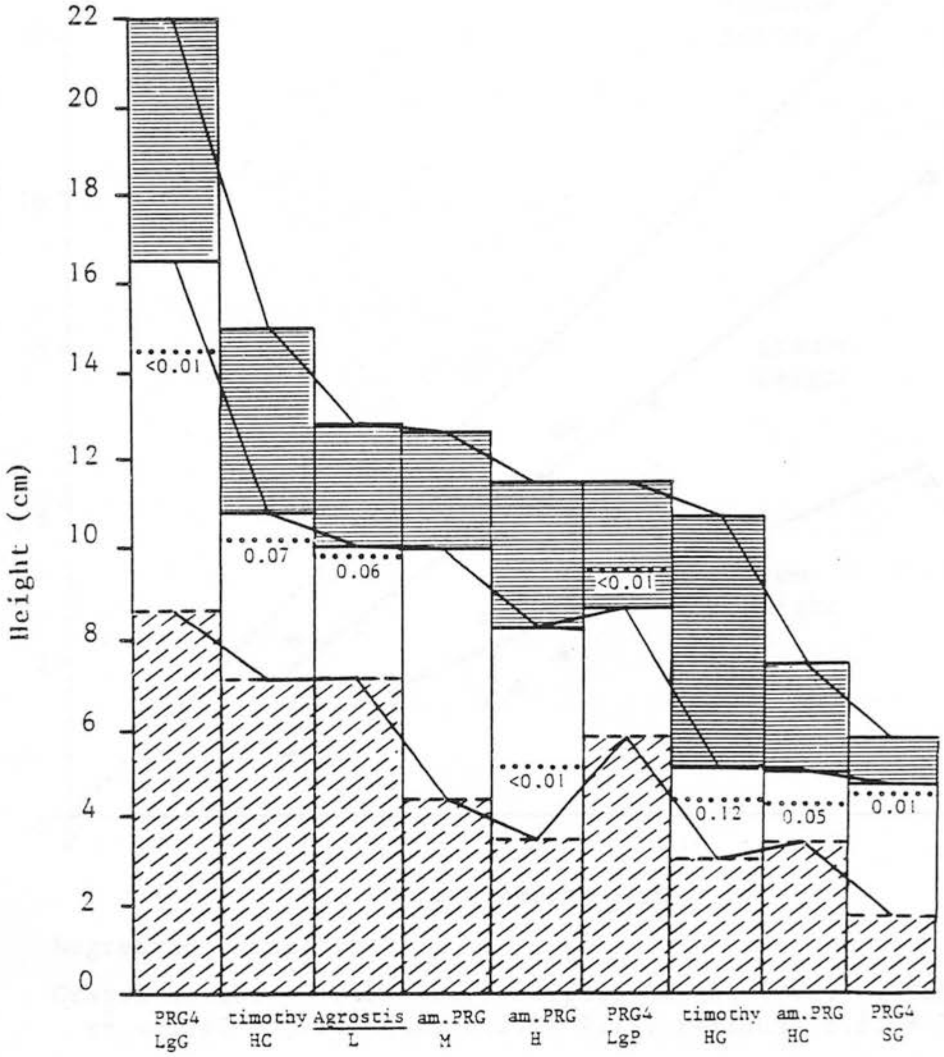
The grass swards sampled in Experiment 2 all had a leafy surface stratum and as they were only grazed for a short time the question of selecting leaf from around pseudostem did not arise. However, an interesting question was whether bite depth was limited by the presence of pseudostem acting as a barrier at a certain height in the sward.

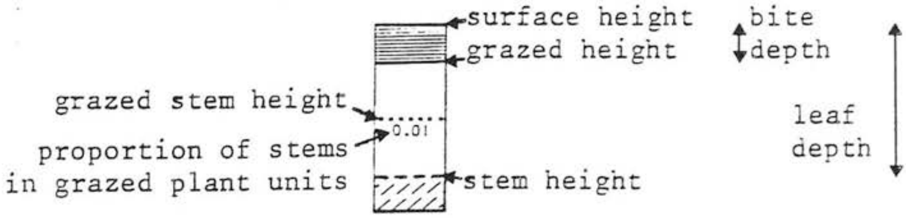
This was investigated initially by setting out in diagrammatic form (Figure E2.17) the relevant height measurements for each sward, in order of descending surface height. The measurements were: mean surface height and stem height (measured before grazing); and mean grazed height and grazed stem height (sward mean values corrected for any missing values). Mean grazed leaf height was not illustrated as it fell within 0.1cm of mean grazed height. The measurements given defined leaf depth and bite depth, and the mean proportion of stems in the grazed plant units was noted for each sward (corrected sward mean values).

Figure E2.17 shows that as surface height declined between swards, mean grazed height also declined, with the exception of a slight rise between am. PRG H and PRG4 LgP. At the same time, mean stem height showed an overall tendency to fall, although there were exceptions to the trend - most noticeably the rise between am. PRG H and PRG4 LgP. Due to the relative rates of decline in these three height variables, bite depth tended to fall both as swards became shorter

Figure E2.17

The interrelationships between mean sward surface height, bite depth, leaf depth and associated variables, over the nine grass swards

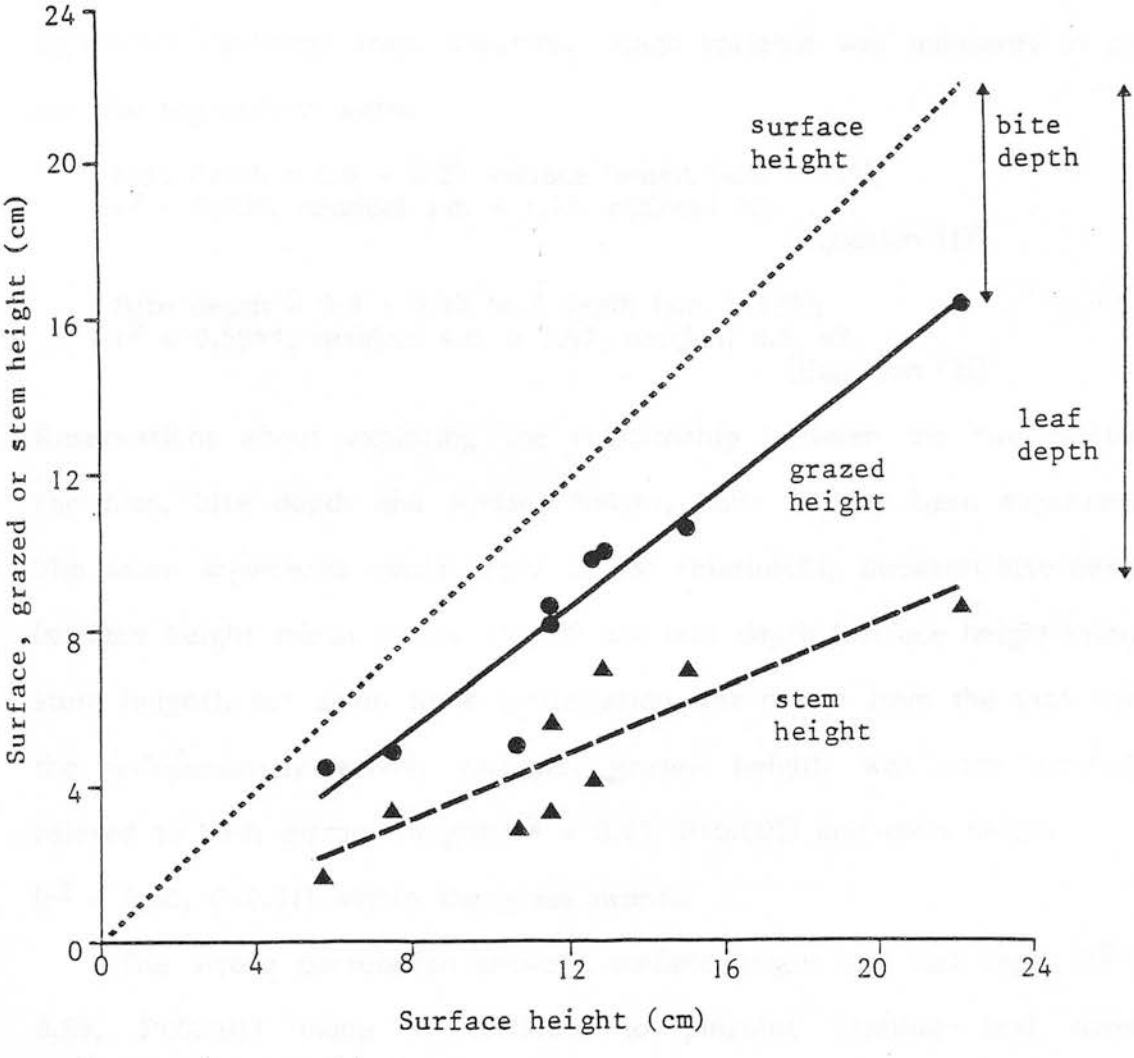




Note: no stems were grazed on am. PRG M.

Figure E2.18

The relationships between mean sward surface height, grazed height and stem height, over the nine grass swards



Regression equations:

Grazed height = $-0.6 + 0.77$ surface height (s.e. 0.085); $r^2 = 0.92^{***}$, residual s.d. = 1.13, residual d.f. = 7.

Stem height = $- 0.3 + 0.43$ surface height (s.e. 0.093); $r^2 = 0.75^{**}$, residual s.d. = 1.23, residual d.f. = 7.

and as leaf depth was reduced. These relationships are also shown in Figure E2.18.

Regression analysis indicated that bite depth was significantly related to either surface height or leaf depth, with no evidence of a significant deviation from linearity. Each variable was measured in cm and the regressions were:

Bite depth = 0.6 + 0.23 surface height (s.e. 0.085);
r^2 = 0.50*, residual s.d. = 1.13, residual d.f. = 7.
[Equation (1)]

Bite depth = 0.5 + 0.40 leaf depth (s.e. 0.125);
r^2 = 0.59**, residual s.d. = 1.02, residual d.f. =7.
[Equation (2)]

Reservations about exploring the relationship between the two related variables, bite depth and surface height, have already been expressed. The same arguments would apply to the relationship between bite depth (surface height minus grazed height) and leaf depth (surface height minus stem height), but again some justification was drawn from the fact that the independently-derived variable, grazed height, was very strongly related to both surface height (r^2 = 0.92, P<0.001) and stem height (r^2 = 0.80, P<0.01) within the grass swards.

The strong correlation between surface height and leaf depth (r^2 = 0.84, P<0.001) made it difficult to pinpoint whether leaf depth determined bite depth, or if the causative variable was either surface height per se or some other canopy structure variable closely associated with surface height. Nevertheless, the slope in Equation (2) was found to be significantly less than one whilst the intercept did not differ significantly from zero, and the regression indicated that on average the sheep grazed less than half the mean leaf depth available. This suggested that bite depth was not constrained primarily by the presence of pseudostem over the range of variation in leaf depth observed in this study.

This view was supported by a comparison of two particular swards illustrated in Figure E2.17. Sheep grazed to a similar depth on am. PRG M and Agrostis L which had similar surface heights but very different stem heights. Moreover, none of the three sheep which sampled the am. PRG M sward grazed any stem whereas on the Agrostis L an average of six stems were grazed per 100 grazed plant units. This suggested that any possible signal to the sheep to limit bite depth did not come from harvesting a few stems, at least on the am. PRG M sward where there was scope for a deeper bite before encountering stem.

Figure E2.17 indicates two further aspects of interest in relation to the grazing of grass swards. Firstly, the mean grazed stem height was always greater than the mean (ungrazed) stem height. This was undoubtedly a reflection on sward canopy structure ; even totally indiscriminate grazing from the sward surface down would result in the tallest stems being grazed first. Secondly, mean grazed stem height was, on all swards except the PRG4 LgP, lower than the mean grazed height (which was close to mean grazed leaf height). This was not surprising as stems would only be likely to be grazed by the deeper bites taken on a particular sward and possibly only by the deepest part of a particular bite. The PRG4 LgP sward was interesting as it had a higher recorded mean grazed stem height than mean grazed leaf height, but as only a very small number of stems were grazed it would be misleading to attach too much importance to this result. Also, as mentioned before, this was the only grass sward to be pre-cut (at 10cm) and it is possible that a few cut stems were wrongly assessed as having been grazed. Even if this were the case, the degree of distortion on the measurement of overall mean grazed height would be negligible as so few stems were involved.

Since the investigation of bite depth in the grasses indicated that whilst leaf depth might have had a minor effect it was not of overriding importance, alternative explanations were sought. Diagrams illustrating sward canopy structure, surface height and grazed height for each sheep (unsmoothed data) on each of the grass swards were examined (Appendix Figures E2.1i-q). These indicated that grazed height for one or more sheep on a sward was often around or just above the upper limit of the stratum containing stem and/or brown leaf. Brown leaf might therefore have been an alternative or additional sward characteristic to pseudostem in limiting bite depth on vegetative swards, but the evidence presented by this set of data was inconclusive.

In widening out the range of swards under consideration to include the oats as well as the grasses, a comparison of the bite depth/surface height regression for the grasses (Equation (1) on p231) with that for all seventeen swards (Equation (1) in Table E2.6) indicated a similar relationship. Neither the intercept nor the slope differed significantly between the two data sets. As might be expected, the inclusion of the tall oats swards had the effect of strengthening the relationship and increasing the proportion of variance accounted for (r^2 = 0.94, P<0.001 for all seventeen swards, compared with r^2 = 0.50, P<0.05 for the grasses).

Conversely, although bite depth was strongly related to leaf depth over the grass swards (r^2 = 0.59, P<0.01), the relationship over all seventeen swards was not significant (r^2 = 0.08). This was not surprising since even if an oats sward did present a positive mean leaf depth, this was not equivalent to a positive leaf depth on a grass sward. The grasses had an entirely leafy surface stratum above a pseudostem-containing layer, whereas the oats had both leaf and stem throughout the sward profile; and while the sheep grazed predominantly on leaf on the grasses, they appeared to have been actively selecting stem on the majority of the oats swards.

Given that the presence of stem did not limit bite depth on the oats swards, Appendix Figures E2.1a-h were examined for other possible causes. No obvious structural characteristics appeared to be responsible, and for example the presence of brown leaf did not seem to have a consistent effect on grazed height on the different oats swards.

Discussion

In this section, the results of the cage trials in Experiment 2 are considered in relation to the available information on bite dimensions and bite weight, and their responses to sward canopy structure. Since the detailed grazing trials run by Black and Kenney (1984) provide the most relevant data for comparison, a short description of this work, including a comparison of its merits with those of the cage trials, is given first.

Black and Kenney (1984) constructed artificial pastures by threading the top two leaves of vegetative tillers of Wimmera ryegrass (Lolium rigidum) through small holes in wooden boards. The bases of the tillers were fixed to the underside of the boards. Tiller density was varied by altering hole spacing and placing 1-3 tillers in each hole; sward height depended on the length of tiller left protruding through the hole. As the leaves used for each board had been trimmed to provide tillers of constant length, a similar surface was exposed for grazing regardless of sward height, although the swards did differ in that only the tallest swards (18-22 cm) had any pseudostem above board level.

The artificial pastures, covering an area of between 285 and 1330 cm^2, were grazed one at a time for 30 seconds by Merino ewes in small pens. Bite measurements were related to various sward measurements - sward height, tiller density, herbage mass and mean sward bulk density (herbage mass divided by surface height). The bite measurements included bite rate (recorded manually), bite weight (calculated from the change in pasture weight during grazing, converted to DM terms and divided by the number of bites), and the product of these two variables, the rate of intake. Bite depth (pre-grazing height minus grazed height) was measured on a limited number of swards, and the area effectively covered by a bite was estimated retrospectively from measurements of bite weight, herbage mass and hole density. Bite volume was not measured.

In many respects, the approach taken by Black and Kenney (1984) was complementary to the approach taken in the cage trials, which were run in the same year. The artificial pastures had certain advantages as they allowed the complete dissociation of sward height and density, and enabled grazing responses to be studied over a wide range of conditions. Since the artificial pastures were very uniform in terms of maturity, chemical composition and herbage composition (apart from the quantity of pseudostem), relationships between bite and sward measurements were unlikely to have been complicated to any great extent by diet selection. In addition, the calculation of bite weight from the change in pasture weight was probably the most accurate method of estimating this variable in short-term experiments.

Notwithstanding the clear advantages of this approach, it had its drawbacks too. Due to the time taken in pasture preparation, the number of pastures sampled was limited, only two sheep were used, and the pasture areas were comparatively small which might have influenced grazing behaviour. In addition, the grazing of an artificial pasture was likely to be very much simplified compared with grazing even a single species "natural" sward on which ingestive behaviour might be influenced by the presence of significant quantities of stem and dead material - and by other characteristics of the sward, soil or environment. Although the approach taken in the cage trials lacked the extreme control over sward characteristics that could be achieved using artificial pastures, it had the strong advantage of using natural swards, grazed under relatively controlled conditions.

Whilst it was not possible to achieve completely independent variation in sward height and density between the natural swards used in Experiment 2, there was a high degree of dissociation between surface height and most of the density variables, particularly grazed stratum bulk density (r^2 = 0.01, n.s.). Therefore the problem of confounding of these variables, experienced to some degree in virtually all of the previous work involving large plot grazing trials, was largely circumvented in the cage trials by comparing bite responses between swards with a wide variety of height/density combinations. The approach relied upon the use of different gramineous forage species, sown at different seed rates and subjected, in some cases, to either grazing or cutting pre-treatments. Even within the eight oats swards or the nine grass swards, the correlation between surface height and grazed stratum bulk density was not significant (r^2 = 0.09 and 0.04 respectively) and on the whole the key relationships between bite responses and sward variables appeared to hold consistently over the different crops. Exceptions such as the relationship between bite area and surface height within the grasses, where there would appear to be a confounding effect of some undescribed characteristics of the individual grass species, are discussed later.

Table E2.13 shows that the range of sward conditions studied in Experiment 2 and in the artificial pasture trials run by Black and Kenney (1984) were broadly similar. Herbage mass and mean sward bulk density covered a greater range in the artificial pastures, while surface height and tiller density both had lower minima but also much lower maxima than the cage swards. In particular no artificial swards over 22 cm in height were studied. Black and Kenney did not measure the bulk density of the grazed stratum, but since the artificial pastures had two leaves per tiller reaching virtually throughout the sward profile, it would be expected that the density within the grazed stratum would not differ greatly from the mean density of the whole sward. The exception might be those swards 18-22 cm in height which had some pseudostem at the base of the profile.

Table E2.13

The range of sward conditions studied in the cage trials (Experiment 2) and in the artificial pasture trials (Black and Kenney, 1984)

	Cage trials	Artificial pasture trials
Herbage mass (kg DM ha^{-1})	300-4200	40-7600
Surface height (cm)	6-55	1-22
Mean sward bulk density (mg DM cm^{-3})	0.33-3.04	0.07-4.23
Grazed stratum bulk density (mg DM cm^{-3})	0.10-2.07	not measured
Tiller density (no. m^{-2})	600-36100	300-26000

Sward conditions studied in the cage trials were also broadly comparable with conditions in previous large plot grazing trials, although as indicated in Table 1 in the Literature Review, the temperate and tropical swards on which cattle bite weight has been measured have tended to have a greater herbage mass and surface height and a lower bulk density in the grazed or surface stratum than the cage swards.

Table E2.14

Bite dimensions and bite weight in different experiments; the range in values and relationships with sward surface height and grazed stratum bulk density (All data are for sheep unless stated otherwise)

Bite measurement	Sward type[t]	Range in values	Relationship[u] with surface height	Relationship[u] with grazed stratum bulk density[v]	Reference
bite depth (cm)	g	1.1 - 5.6	+	n.s.	Experiment 2
	g + o	1.1 - 21.0	+	n.s.	Experiment 2
	ag	9 - 16[w]	n.e.	-[w]	Black and Kenney (1984)
	g	0.3 - 11.9	+	n.e.	Forbes (1982a)
	g/c	0 - 6.5[w]	+	n.e.	Milne *et al* (1982)
bite area (cm^2)	g	9.4 - 21.8	+ within crops	n.s.	Experiment 2
	g + o	9.3 - 36.8	n.s.	n.s.	Experiment 2
	ag	8.6 - 33.0	n.e.	-[w]	Black and Kenney (1984)
bite volume (cm^3)	g	10 - 109	+	n.s.	Experiment 2
	g + o	10 - 495	+	n.s.	Experiment 2
	ag	11 - 471[w]	+[w]	-[w]	Black and Kenney (1984)
bite weight (mg DM)	g	40 - 158	+ (n.s.)	+	Experiment 2
	g + o	40 - 329	+	+ (n.s.)	Experiment 2
	ag	10 - 200	+	+[w]	Black and Kenney (1984)
	g	25 - 420	+[x]	n.e.	Allden and Whittaker (1970)
(mg OM)	g	11 - 400			Hodgson (1986)[y]
	g		+		Hodgson (1981a), Forbes (1982a), Penning (1986)
	g			+ cattle	Stobbs (1973b, 1975b)

t Sward types: g grass, g + o grass and oats, ag artificial grass pasture, g/c grass/clover mixture
u Relationships: + positive, - negative, n.s. not statistically significant ($P \geqslant 0.05$), n.e. not examined
v Black and Kenney (1984) quoted relationships with mean sward bulk density
w derived from data or figures presented in the reference
x Allden and Whittaker (1970) quoted the relationship with tiller length
y summary of data from several temperate sown swards

Bite measurements

Bite depth. As in the trials reported by Arnold (1964), Forbes (1982a), Milne et al (1982), Barthram and Grant (1984) and presumably also Black and Kenney (1984), the sheep in Experiment 2 appeared to graze the sward from the surface down. Table E2.14 shows that bite depth on the cage grasses fell within the range of values recorded in other experiments, but the maximum value on an oats swards, 21 cm, lay outside the range. The highest value previously recorded was 16 cm (Black and Kenney, 1984).

Bite area. Bite area on the grasses sampled in Experiment 2 was measured directly on the sward surface and was considered to be limited by mouth dimensions, herbage length and/or the forces required to harvest a bite. On the much sparser oats swards and on Black and Kenney's artificial pastures, however, bite area was a measure of the area effectively covered by a bite and was calculated retrospectively from a knowledge of the population density of plant units or tillers. By definition, all else being equal, the area effectively covered by a bite increases as the sward becomes sparser and the plant units fewer and further apart. Results from the oats cage trials and the artificial pasture trials indicated very similar ranges in the area effectively covered by a bite, while true bite area on the cage grasses had a similar minimum value (9 cm^2) but lower maximum value (22 cm^2 compared with 37 cm^2 on the oats and 33 cm^2 on the artificial pastures) (Table E2.14).

In measuring both bite depth and bite area in Experiment 2, it was assumed that bites did not overlap in the sward and therefore that the dimensions measured were those of the average individual bite. However, this might have been an oversimplification. Although observations of grazing activity did not detect sheep taking successive bites on the same herbage, the data on the mean number of grazed plant units per bite (mean sward values presented in Tables E2.8 and E2.9 for the grasses and oats respectively) indicated that this might have occurred, to some degree, on the oats swards. Whereas each of the 33 grass cage patches sampled had on average at least nine severed plant units per bite taken, in five of the 29 oats cage patches which were sampled the number of bites taken (20 to 22) exceeded the recorded number of grazed leaves and stems by a number ranging from one to five. It was unlikely that the number of harvesting bites was miscounted, and therefore since the sheep must have severed at least one plant unit at each harvesting bite, it would appear that on at least some - and possibly all - of the oats swards either some grazed plant units were not recorded or the sheep took successive bites on the same tiller, perhaps even the on same leaf or stem.

The consequences of overlapping bites would be that mean bite depth would be overestimated (the measurement of bite depth really being that of grazed depth) while mean bite area would be underestimated. Bite volume might or might not be affected.

It was not possible to quantify, or correct for, the possible errors in the bite depth and bite area measurements on the oats. However, since the overlapping of bites was not thought to have been a problem on the grass swards and since the key relationships involving bite depth and bite volume, if not bite area, did not differ significantly between the oats and the grasses, any errors in the measurement of the oats bite dimensions were unlikely to have had an undue influence on the results.

Bite volume. Bite volume in the cage trials was calculated as the product of bite depth and bite area, whether bite area was measured directly on the sward (grasses) or was a measure of the area effectively covered by a bite (oats). Due to higher values for both bite depth and bite area, the maximum bite volume on the oats (495 cm^3) was over four times the maximum bite volume on the grasses (109 cm^3) (Table E2.14). There are no published figures for bite volume in the literature with which to compare the cage results, but it is possible to derive estimates from the data quoted by Black and Kenney (1984). If it is assumed that mean sward bulk density equalled the bulk density of the grazed stratum, then bite volume may be estimated by dividing bite weight by mean sward bulk density. Thus, bite volume would have ranged from approximately 11 cm^3 on a sward 1 cm high with a mean sward bulk density of approximately 1.3 mg DM cm^{-3} (bite weight 14 mg DM) to approximately 471 cm^3 on a sward 18 cm high with a mean sward bulk density of 0.07 mg DM cm^{-3} (bite weight approximately 33 mg DM). As indicated in Table E2.14, this range in bite volume values was very similar to the range over all seventeen cage swards.

Bite weight. Since the sheep used in Experiment 2 were fasted for sixteen hours before sampling, and were then allowed only 20 bites from a cage patch, it was considered that the animals would have been hungry and attempting to maximise bite weight within the limitations imposed by sward conditions. Similarly, the sheep used by Black and Kenney (1984) were also considered to have been hungry. Chacon and Stobbs (1977) found that oesophageal fistulated cows had a greater bite weight after fasting for sixteen compared with two hours, but these workers considered that bite weight was influenced more by sward canopy structure than by fasting.

The range of values for bite weight on the cage grasses (40-158 mg DM) lay within the ranges quoted for other experiments (Table E2.14). The maximum value on an oats swards (329 mg DM), whilst lying within the bite weight ranges quoted in the literature for natural grass swards, was greater than the maximum value of 200 mg DM reported for the artificial grass pastures.

Allowing 20 bites per cage patch was a compromise; fewer bites would have reduced the risk of bites overlapping and causing errors in the bite dimension measurements, whilst a larger number of bites would probably have increased the accuracy of the bite weight estimate. The coefficient of variation (CV) for bite weight over all seventeen cage swards was 0.24. This was in line with the CV for sheep and cattle bite weights calculated from extrusa collection in large-scale trials on sown swards (0.18-0.29; Jamieson, 1975) and an improvement on the corresponding CV from trials on indigenous swards (0.48; Forbes, 1982a). In addition, the extrusa-based estimate of bite weight in Experiment 2 was in reasonably close agreement with the sward-based estimate (bite volume multiplied by grazed stratum bulk density), giving confidence in the technique of using fistulated sheep to estimate bite weight.

The interrelationships between sward variables, bite dimensions and bite weight

Relationships with bite depth

As indicated in Table E2.14, the strong positive linear relationship between bite depth and surface height in Experiment 2 was also observed in trials run by Forbes (1982a) and Milne et al (1982). Milne et al (1982) grazed sheep for 30 minutes on grass/clover swards covering an area of 100 m^2 and ranging in height from approximately 6 to 19 cm, whilst Forbes (1982a) grazed sheep for 15-20 minutes on plots only 18 m^2 in area, but supporting various grass crops which ranged in height from 5 to 32 cm. In the cage trials, sheep were allowed to take 20 bites from patches of grass or oats swards only 0.26 m^2 in area, but ranging in height from 6 to 55 cm. Different measurement techniques were also used in the three experiments, but both Milne et al (1982) and Forbes (1982a) obtained similar linear regressions to the cage trials for the relationship between bite depth and surface height (Equation (1) in Table E2.6). The slopes of the regression lines did not differ significantly and the intercepts also appeared similar, although they could not be subjected to a statistical test. The greatest proportion of variance accounted for by the relationship was in the cage trials (0.94, $P<0.001$) followed by Forbes' trial (0.88, $P<0.001$) and the trial run by Milne et al (0.59, $P<0.001$).

Barthram and Grant (1984) found a positive relationship between grazed depth and the pre-grazing leaf height. Sheep which grazed over a period of weeks on short (1.7-4.8 cm) vegetative swards dominated by ryegrass, grazed to a depth of 0.5-2.4 cm (G.T. Barthram, personal communication) and the limit of the depth of grazing was associated with the upper extent of the pseudostem. However, the presence of pseudostem did not appear to be a major factor in limiting bite depth in the taller grasses grazed in the cage trials. Milne et al (1982) also considered it unlikely that pseudostem restricted bite depth in their relatively tall grass/clover swards.

The results of an examination of Appendix Figures E2.1a-q for sward characteristics which might have limited bite depth in the oats and grass swards were inconclusive. The presence of brown leaf might have been involved in the grass swards, but this component did not appear to affect bite depth consistently in the oats. Other sward or animal factors which were not measured in the experiment might have been responsible for, or contributory to, the limitation of bite depth. One might speculate that within a given sward, bite depth might be limited by factors such as: the increase in the force required to sever a mouthful of herbage (a deeper bite is likely to encompass more plant units, with a greater tensile strength, even if these units are all leaves); the length of leaf or stem which sheep find comfortable to manipulate;

and the presence of fungal infection at lower levels in the sward.

Although Black and Kenney (1984) did not measure bite depth on pastures of different height, they did find a negative relationship between bite depth and tiller density or mean sward bulk density (and hence presumably also grazed stratum bulk density) on pastures at a constant height of 18.0 cm. These workers did not quote correlation coefficients or regressions for any of the relationships between bite and sward variables, but bite depth increased from 9 to 16 cm as mean sward bulk density fell from 4.23 to 0.07 mg DM cm^{-3}. Presumably on the sparser swards the sheep were able to graze deeper because they prehended fewer leaves at a bite, but as there was a concomitant decline in bite weight the increase in bite depth was clearly inadequate to compensate for the fall in sward density.

It was interesting that on the artificial pastures, where there was leaf virtually throughout the sward profile, the sheep grazed deeper than on the six cage swards with the most comparable sward heights (Table E2.15).

Table E2.15

A comparison of bite depth on certain cage swards (Experiment 2) and artificial pastures (Black and Kenney, 1984)

	Range in bite depth (cm)	Range in surface height (cm)	Range in grazed stratum bulk density (mg DM cm^{-3})
Cage swards			
oats LP, MP, HP timothy HC	4.3-6.3	15.0-16.6	0.70-1.61
oats HC, PRG4 LgG	5.6-7.2	22.1[a]	0.28-0.59
Artificial pastures			
group 2	9-16	18.0[a]	0.07-4.23[b]

[a] All swards or pastures were the height indicated, i.e. the range was nil

[b] figures quoted for mean sward bulk density

While the smallest bite depth on artificial pastures 18.0 cm high was 9 cm at a mean sward bulk density of 4.23 mg DM cm^{-3}, even the largest bite depth on the six cage swards was only 7.2 cm despite the greater surface height (22.1 cm) and much lower grazed stratum bulk density (0.28 mg DM cm^{-3}). This again suggested that some characteristics of the natural swards inhibited bite depth, but there might also have been differences in the bite depth of the different sheep breeds used in the two experiments.

Relationships with bite area

Over all seventeen cage swards, and over the set of fourteen swards excluding the three tall oats swards, bite area was not significantly correlated with any sward variable. However, when the data set was restricted to the nine grass swards on which bite area was measured directly, there was a strong overall relationship between bite area and herbage mass but not surface height or any of the density variables. This could have been a genuine finding, with the sheep responding to the presumably visual cue of the quantity of herbage present per unit area of ground, or it could have been due to herbage mass acting as a dummy for some combination of height and density variables - although multiple regression analysis failed to detect this.

Figure E2.12 indicated that the relationship between bite area and surface height in the grass swards was confounded by individual crop effects. The positive relationship within a grass species was probably due to the sheep being able to gather together a greater number of longer plant units before severing a mouthful of herbage. Provided that after the bite was taken the grazed surfaces of at least some of the grazed units returned to their original positions in the sward, the bite area measurement would be greater on taller swards. The gathering process need not be complicated and time-consuming; herbage could be quickly gathered by a scooping action with a partly horizontal movement of the head rather than a plucking action in a predominantly vertical plane.

The relationship between bite area and the population density of grazed plant units on the grass swards was also of interest (Figure E2.13). Although failing to reach statistical significance, the relationship appeared to be negative, at least within grass crops. Were bite area restricted by a limited force expenditure per bite, as proposed by Hodgson (1985a) and Hughes (unpublished), then a negative relationship would be expected within a grass species. In addition, the number of grazed plant units per bite would be relatively constant within a species. Although the grass swards did generally conform with these two conditions, one of the nine swards (PRG4 LgP) did not. It was concluded that there were insufficient data for a firm conclusion to be reached about the validity of the theory of a summit force per bite limiting bite area. Clearly, the number of observations on grass swards was limited, and in order to resolve the question of which sward variables determine bite area a greater number of swards would need to be sampled.

The area effectively covered by a bite decreased with increasing tiller density, and presumably also grazed stratum bulk density, in the artificial pasture trials (Table E2.14). It also decreased with an increase in either the population density of grazed plant units or the bulk density of the grazed stratum on the cages oats swards. However, such relationships on the oats and artificial pastures were only to be expected from the way in which bite area was calculated. The relationships between bite area and herbage mass, surface height and the population density of grazed plant units on the cage grasses were of greater importance.

Relationships with bite volume

The investigation of the interrelationships between the bite dimensions in Experiment 2 indicated that of the two components of bite volume, bite depth and bite area, it was bite depth which had the greater influence on bite volume. Bite depth and bite area were themselves very poorly related.

Following on from the strong positive linear relationship between bite depth and surface height, bite volume was also strongly related to surface height on the cage swards. Bite volume estimated from Black and Kenney (1984) was related positively to sward height and negatively to mean sward bulk density (Table E2.14). This negative relationship was to be expected in view of the negative relationships found by these workers between mean sward bulk density and both bite depth and bite area. Although over all seventeen cage swards the relationships between each bite dimension and grazed stratum bulk density also tended to be negative, they were negligible ($r^2 \leqslant 0.04$, n.s.).

Relationships with bite weight

Bite weight was strongly positively related to bite depth and bite volume over all seventeen cage swards (Table E2.5a), although the relationships were not significant when the three tall oats swards were excluded from the data set (Table E2.5b). Bite weight and bite area were positively but not significantly related in both data sets.

The selection for stem in a horizontal plane demonstrated on all but one of the oats swards (Table E2.9) was surprising, as was the lack of any significant effect of this selectivity on bite weight or any of the bite dimensions. In previous work, animals have usually been shown to select for gramineous leaf rather than stem, and in trials on tropical swards this selectivity has been shown to lead to a decline in bite weight (Stobbs, 1973b; Chacon and Stobbs, 1976). In the tropical grasses studied by these workers, the nutritional quality of the stem was markedly lower than that of the leaf. There was probably far less contrast between leaf and stem in the oats grazed in Experiment 2 and this, together with the fact that it might have been to the advantage of the hungry sheep to select the heavier plant units (stems) in the relatively sparse swards, could have accounted for the unusual selection response. Unfortunately, comparisons could not be drawn with the cage grasses - horizontal selection could not be examined in these swards because they had no stem in the surface stratum.

The key sward variables influencing bite weight in the cage trials were surface height and grazed stratum bulk density (Table E2.14). When the data set included the tallest oats swards, surface height (operating primarily through bite depth and bite volume) had the dominant influence on bite weight (Figure E2.10a). Grazed stratum bulk density on its own had only a minor (non-significant) effect. Conversely, when bite weight was examined over the subset of swards with a reduced surface height range, it was grazed stratum bulk density rather than surface height which on its own significantly influenced bite weight (Figure E2.10b).

In the cage trials, the positive relationship between bite weight and surface height appeared to be linear up to a height of 55 cm, although some clumping of points was apparent (Figure E2.8). Black and Kenney (1984) found that bite weight was still increasing on their tallest swards (22 cm) when the mean sward bulk density was 1.3 mg DM cm^{-3} or less; in denser swards, the maximum bite weight (200 mg DM) appeared to be reached on swards only 6.5 cm tall. These results were not inconsistent with the cage trial results since only two of the seventeen cage swards had a grazed stratum bulk density greater than 1.3 mg DM cm^{-3}.

The linear relationship between the bite weight of sheep and sward surface height has been found in other experiments on swards with a surface height of up to 12 cm (Penning, 1986), 21 cm (Hodgson, 1981a) and 24 cm (Forbes, 1982a). Also, Allden and Whittaker (1970) found that the linear relationship between bite weight and tiller length was still in operation at a tiller length of 37 cm. However, the cage trials appear to be the first experiment in which the linear relationship between sheep bite weight and surface height has been shown to hold up to a height of 55 cm.

Within the subset of fourteen swards, the positive linear relationship between bite weight and grazed stratum bulk density held up to a density of 2.1 mg DM cm^{-3} (Figure E2.9). Black and Kenney (1984), however, illustrated a curvilinear response to increasing tiller density, and hence presumably also to increasing grazed stratum bulk density. After an initial sharp rise, the bite weight response began to flatten out, but bite weight was still increasing slightly at the maximum mean sward bulk density of 4.2 mg DM cm^{-3}. These results from the cage and artificial pasture trials contrasted with cattle bite weight responses measured by Stobbs (1973b, 1975b). Bite weight in cows increased up to a grazed stratum bulk density of only 0.22-0.32 mg DM cm^{-3} and then either remained constant with further increases in density (Stobbs, 1975b) or alternatively declined (Stobbs, 1973b). However, Stobbs' trials were run under less controlled conditions than either the cage or artificial pasture trials, and changes in sward density were confounded with changes in sward height and quality. In Stobbs (1973b) for example, the decline in bite weight at high sward densities was almost certainly due to the increase in sward maturity and hence stemminess.

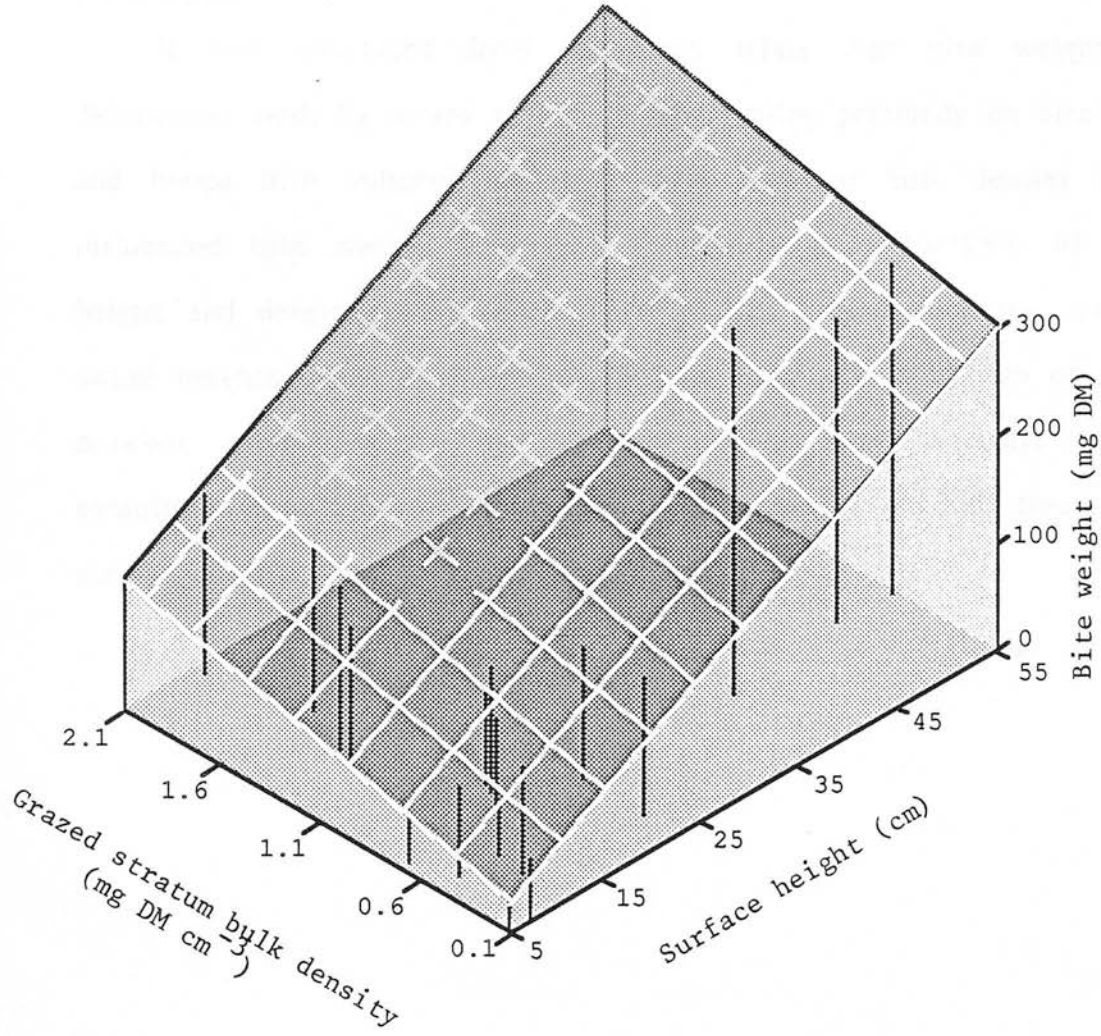
Regression analysis on the cage trial data showed that multiple regressions relating bite weight to surface height and grazed stratum bulk density were an improvement upon both the bite weight/surface height relationship over all seventeen swards, and the bite weight/grazed stratum bulk density relationship over the fourteen swards. For each data set, the addition of the interaction term failed to give a further significant improvement, demonstrating that the effects of sward height and density on bite weight were independent. Since an examination of the multiple regression equations indicated that the three tall oats swards formed part of the same response continuum as the fourteen shorter swards, the equation for all seventeen swards was used to illustrate the response surface (Figure E2.19).

When examining this figure, it should be noted that whilst the seventeen swards were adequate to define the bite weight response over comparatively short swards ranging widely in density, and over comparatively sparse swards ranging widely in height, bite weight was not measured on swards which were both tall and dense. (Gramineous swards with both these characteristics would be difficult, if not impossible, to grow). Consequently, the response surface was extrapolated to cover such conditions, with a predicted maximum bite weight of 390 mg DM on swards 55 cm high with a bulk density in the grazed stratum of 2.1 mg DM cm^{-3}. This figure lies within the range of bite weight values quoted for sheep by Allden and Whittaker (1970) and Hodgson (1986) (Table E2.14).

Figure E2.19 and the attendant multiple regression equation indicate that at the mean surface height of 19.3 cm, a doubling of grazed stratum bulk density would lead to bite weight increasing by a factor ranging from 1.04 (density 0.20 compared with 0.10 mg DM cm^{-3}) to 1.3 (density 2.07 compared with 1.03 mg DM cm^{-3}). Conversely, at the mean grazed stratum bulk density (0.79 mg DM cm^{-3}), a doubling of surface height would cause bite weight to increase by a factor ranging

Figure E2.19

The combined effect of sward surface height and grazed stratum bulk density on bite weight



Bite weight = −4.9 + 5.5 surface height (s.e. 0.63)
+ 44.2 grazed stratum bulk density (s.e. 17.9)

$r^2 = 0.85^{***}$

from 1.5 (surface height 10.0 compared with 5.0 cm) to 1.8 (surface height 55.0 compared with 27.5 cm). This illustrates once again that over the complete range of swards studied, surface height had a greater relative influence on bite weight than had grazed stratum bulk density, but both these sward variables were important.

Conclusions

It was concluded from the cage trials that bite weight was determined both by sward surface height (acting primarily on bite depth and hence bite volume) and by grazed stratum bulk density (which influenced bite weight directly). The relative importance of sward height and density in influencing bite weight varied with the range of sward heights under consideration, but by examining a variety of swards between which height and density varied simultaneously, it was established that these variables acted independently and that there was a simple, additive, planar joint response surface.

GENERAL DISCUSSION

In this section, the main results are summarised for Experiments 1 and 2, comparisons are drawn where appropriate, and the new findings are considered within the framework of existing knowledge of the grazing animal's behavioural responses to changes in sward canopy structure. The relative merits of the two contrasting approaches taken in the current work are discussed, and suggestions are made for further research.

Bite weight and bite dimensions

Experiment 1, the series of conventional large plot grazing trials, confirmed the finding from previous work that bite weight was the main behavioural determinant of both the short-term rate of intake and daily herbage intake. Bite rate and grazing time were negatively related to intake; they tended to increase as bite weight declined, but not enough to maintain the level of intake.

Two different measurement techniques were used to estimate bite weight in the current experiments. Bite weight was derived from the estimate of herbage intake in Experiment 1, but measured directly using oesophageal fistulated sheep in the series of cage trials comprising Experiment 2. In addition, bite weight was expressed relative to live weight in Experiment 1 where the sheep were young and still growing, but in Experiment 2 bite weight was expressed in absolute terms because the relatively small proportional increases in live weight of the older sheep over the experimental period were attributed to an increase in body condition rather than skeletal size. In order to compare bite weight between experiments, the values obtained in the cage trials were converted from mg DM to mg OM kg LW^{-1}, using the mean live weight figure of 74.5 kg and assuming that the proportion of OM in the herbage DM in the extrusa was 0.90. A similar range of values was obtained in both experiments; 0.48-3.97 mg OM kg LW^{-1} in the cage trials compared with 0.31-3.29 mg OM kg LW^{-1} in Experiment 1. The maximum bite weight in the cage trials tended to support the maximum value in Experiment 1 which was high compared with previous work.

Both experiments indicated the importance of bite depth in influencing bite weight. The positive linear relationship was stronger under the more controlled conditions of the cage trials (Equation (3) in Table E2.6), but when this equation was adjusted in order to express bite weight per kg live weight it did not differ significantly from the corresponding regression equation for the subperiod 1 data in Experiment 1. Data for subperiod 1 were the most relevant for a comparison with the cage data since both were reliant on a between-sward comparison only, and in the large plot trials the effects of trampling and sward contamination would be least over the first subperiod.

The consistency of the bite weight/bite depth relationship between experiments suggested that differences in the measurement techniques used for each variable were unlikely to have been important.

Bite depth

In Experiment 1, the median bite depth was estimated from observations of the depth of head insertion into the sward (range 1.2-13.1 cm). In the cage trials, mean bite depth was estimated from the difference in sward height before and after grazing and was found to range from 1.1 to 21.0 cm. The greater maximum value in the cage trials appeared to be due to the sampling of taller swards (surface height up to 55 cm) than in Experiment 1 (surface height up to 30 cm in subperiod 1). However, it was recognised that both measurement techniques could overestimate the true bite depth if bites overlapped, i.e. the sheep took successive bites down the same tillers.

A positive linear relationship between bite depth and surface height held for each experiment. Once again, the relationship was stronger in the cage trials (Equation (1) in Table E2.6) and the regression equations for the cage trials and for subperiod 1 in Experiment 1 did not differ significantly. Over these two regressions and the regressions quoted by Forbes (1982a) and Milne et al (1982) for the relationship between bite depth or grazed depth for sheep and sward surface height (both measured in cm), the slope of the height term varied only from 0.33 to 0.42 and did not differ significantly. The intercept ranged only from -1.6 to +1.2 cm. Therefore, the relationship was relatively stable in different situations, over the range of heights investigated. An increase in surface height of between 2.4 and 3.0 cm resulted in an increase in bite depth of 1.0 cm.

In addition to surface height, diet digestibility influenced bite depth in Experiment 1. The sheep grazed deeper on taller, more digestible swards (Table E1.21). Diet digestibility was not measured in the cage trials, but since the linear regression with surface height accounted for 0.94 of the variance in bite depth it was doubtful whether the inclusion of a term for diet digestibility would have resulted in a significant improvement.

Diet digestibility in Experiment 1 was considered to have acted as a dummy variable for some combination of sward properties, but it was not possible to conclude from the current experiments whether any particular structural characteristics limited bite depth. Pseudostem height, which has been found to limit the depth of grazing in very short vegetative swards (Barthram and Grant, 1984), did not appear to have a major influence on bite depth in the taller vegetative swards sampled in the cage trials. The presence of brown or dead material at the lower levels of the sward profile might have had an effect, but since in

Experiment 1 the lower limit of the grazed stratum generally decreased between successive subperiods, sometimes reaching ground level, it was clear that the factors which governed bite depth altered with the stage of defoliation.

In addition to changes in the herbage composition, mechanical properties and nutritional quality of a sward as it was grazed down, the appetite drive of the animal would also be likely to change during the course of a long-term trial, and these variables could all influence the threshold "acceptability" level down to which the animal grazed. The fact that the decrease in the lower limit of the grazed stratum with time in Experiment 1 was accompanied by a concomitant decline in the depth of that stratum (or bite depth) would suggest that whilst the animal was prepared to reduce the threshold "acceptability" level and graze herbage of a lower quality, it was either not prepared to take such deep bites, or not capable of doing so. This clearly penalised bite weight, and ultimately also daily herbage intake, since increases in the total daily bites could not compensate.

Bite area and bite volume

The estimates of bite area and volume in Experiment 1, on the eight oats swards sampled in the cage trials, and in the artificial pasture trials of Black and Kenney (1984), were of the dimensions effectively covered by a bite. Except on relatively dense swards, such estimates tend to be determined by the sparsity of the sward rather than by mouth dimensions. As the distance between tillers or plant units (leaves and stems) increases, there is a corresponding increase in the area or volume effectively covered by a bite.

By contrast, true bite area was measured directly on the nine (comparatively dense) grass swards sampled in the cage trials, allowing the direct calculation of true bite volume (the product of bite area and depth). All three bite dimensions on the grass swards were probably determined to some extent by mouth dimensions, although on long herbage bite area might exceed mouth area if the animal were to gather herbage before harvesting it. Bite depth would not be limited by any mouth dimensions if herbage were severed and then drawn gradually into the mouth, but sheep rarely grazed in this manner on the grasses.

The cage trials are the first known experiment in which true bite area and volume have been measured. Over the nine grass swards bite area ranged from 9 to 22 cm^2, bite volume from 10 to 109 cm^3.

Since bite depth varied proportionally to a greater extent than bite area in the cage trials (whether all seventeen swards or just the nine grass swards were considered), bite depth had the greater influence on bite volume. Consequently, bite volume, like bite depth, was positively related to surface height.

The sward variables driving the bite area response were less easily determined. Over all nine grass swards, bite area was positively related to herbage mass but was not significantly related to either height or density. There were, however, indications that within a particular grass species bite area was related positively to surface height and negatively to the population density of grazed plant units. The first relationship would suggest that when the grass was longer the sheep were able to gather a greater number of plant units to sever at a bite. The second relationship would comply with the theory of a limit to force expenditure per bite (Hodgson, 1985a; Hughes, unpublished); there may be an upper limit to the number of plant units of a particular grass species that can be severed at a bite. However, only a limited amount of data was available and the evidence was not conclusive for either of these relationships.

Bite weight

In view of the positive relationships between bite weight and bite depth, and between bite depth and surface height, a positive relationship between bite weight and surface height would be expected. Such a relationship was found for the cage trials (Equation (5) in Table E2.6), and when this equation was adjusted in order to express bite weight per kg live weight it was similar to the corresponding, but weaker, regression equation for the complete data set (both within- and between-sward comparisons) in Experiment 1. The slope of the height term in the regression equation for the cage trials (0.06) did not differ significantly from the corresponding slope for the complete data set in Experiment 1 (0.04) or from the slopes of 0.09 and 0.03 quoted respectively by Hodgson (1981a) and Forbes (1982a) in regression equations relating bite weight in sheep to sward surface height. Nevertheless, the slope of the height term was clearly less consistent between these bite weight/surface height regressions than between the bite depth/surface height regressions discussed previously. The slope of the height termed ranged by a factor of three in the bite weight regressions compared with a factor of 1.3 in the bite depth regressions.

Although the relationship between bite weight and surface height in subperiod 1 in Experiment 1 was also positive, it failed to reach the 0.05 significant level. Diet digestibility, rather than surface height, had the dominant influence on bite weight in both data sets examined in Experiment 1, but in each case the height term was additive at a later stage in the multiple regressions (Table E1.22). Thus, bite weight increased on taller, more digestible swards, presumably via the concomitant increase in bite depth noted earlier.

The effect of diet digestibility on bite weight could not be assessed in the cage trials as this variable was not measured. However, since the grazed stratum bulk density had a significant positive effect on bite weight over and above the effect of surface height (total $r^2 = 0.85$ over the seventeen swards), there was only a comparatively small proportion of residual variance which could have been attributed to diet digestibility.

Surprisingly, the grazed stratum bulk density did not appear to be a major determinant of bite weight in Experiment 1. Indeed the relationship was negative rather than positive, even when the data were restricted to subperiod 1. Such a relationship is most unlikely biologically. The apparent contradiction between the two experiments, and the unexpected result in Experiment 1, might have arisen for the following reasons.

Firstly, whilst the association between surface height and grazed stratum bulk density was negligible in the cage swards ($r^2 = 0.01$, n.s.), it was slightly greater in Experiment 1 ($r^2 = 0.05$, $P<0.05$ in the complete data set; $r^2 = 0.09$, n.s. in subperiod 1). The negative relationship between bite weight and density observed in the latter experiment might have arisen as a consequence of the positive relationship between bite weight and height, and the negative association between height and density.

Secondly, since the experimental conditions were more controlled in the cage trials where a much smaller and more uniform area of herbage was grazed and the various sward and bite measurements were probably measured more accurately, it might be expected that this experiment would give clearer results. Although grazed stratum bulk density, when converted to the same units in both experiments, covered a similar range (0.09 - 1.86 mg OM cm^{-3} in the cage trials compared with 0.07 - 1.81 mg OM cm^{-3} in Experiment 1), this variable in particular was estimated much more directly and without the confounding effects of trampling in the cage trials.

Thirdly, whilst it might be assumed that there was virtually no stage of grazing or time effect when the sheep took only 20 bites from a cage sward, there would have been such an effect in Experiment 1, even when the data were restricted to the first subperiod. Each subperiod lasted from two to four days, during which time there were usually considerable changes in sward conditions and animal responses, and therefore the Experiment 1 data would inevitably have included a dynamic component. Seasonal variation would also be greater in Experiment 1, and running the large plot trials over two different grazing seasons might have introduced a further source of variation.

Another contrast between the two experiments was that whilst features associated with individual crops had a strong influence on bite weight (and on bite depth) over and above the effects of the measured sward variables in Experiment 1, this was not the case in the cage trials.

In Experiment 1, the crop effect accounted for an additional 0.13 - 0.34 of the variance in bite weight or bite depth in the subperiod 1 and complete data sets, after terms for height, digestibility and any significant interactions or quadratics had been fitted (Tables E1.21 and E1.22). The most likely explanation of the crop effect was that it was due to unmeasured sward canopy structure variables, although seasonal variation and variation between years might also have been involved. The intrinsic qualities of the different crop genotypes were unlikely to have been responsible since the indoor feeding trials indicated that none of the quality variables measured had a significant effect on voluntary intake.

Although the lack of a crop effect in the cage trials might be attributed to the narrower range of crops used (five compared with twelve in Experiment 1), these five crops did include strongly contrasting genotypes. It is possible that because the sheep were fasted for sixteen hours before sampling, and were then restricted in the number of bites they could take, hunger overrode any crop effects - and perhaps also diet digestibility effects - in this experiment. Alternatively, sward canopy structure might have had the only true influence on bite responses in both experiments, and the apparent crop effect in Experiment 1 might have reflected the less controlled experimental conditions and poorer estimates of variables such as grazed stratum bulk density and bite weight. Further experimentation would be required to clarify this issue.

In the cage trials where there was the expected positive relationship between bite weight and grazed stratum bulk density, the relative importance of bite volume and the density variable in determining bite weight varied with the range of sward heights under consideration (Figure E2.10). Bite volume, and therefore bite depth and the sward variable surface height, had the dominant influence on bite weight over all seventeen swards. Over the subset of fourteen swards, excluding the three tallest, the grazed stratum bulk density was the major determinant of bite weight.

Over both data sets, the effects of height and density on bite weight were additive with no evidence of curvilinearity or an interaction. Figure E2.19 illustrated the planar response surface obtained for the complete data set, with bite weight increasing linearly as either height or density increased up to comparatively high levels (55 cm and 2.1 mg DM cm^{-3} respectively). On the tall oats swards, the sheep were frequently observed to sever, with a single harvesting bite, long plant units which were then gradually drawn into the mouth by nibbling. Therefore, the linear bite weight/surface height relationship might be expected to hold for even taller swards. The bite weight/grazed stratum bulk density relationship, however, would be expected to level off eventually in very dense swards where the animal had to reduce bite depth and/or bite area in order not to exceed the maximum number of plant units it could sever at a bite. This type of asymptotic bite weight/density response was observed by Black and Kenney (1984), for sheep grazing artificial pastures.

Even over the range of sward heights or densities which produced a linear increase in bite weight, the pattern of response in daily herbage intake would probably be asymptotic rather than linear, due to the typical compensatory reduction in total daily bites at high bite weights. Most previous grazing trials on temperate swards have indicated a positive linear relationship between surface height and bite weight, but an asymptotic relationship with daily herbage intake.

The Literature Review indicated an apparent contradiction between the sward variables which have been found to determine bite weight on temperate and on tropical swards. Sward bulk density, leaf bulk density and leaf content have usually been considered the key variables on tropical swards, rather than sward height as in the case of temperate swards. Table 1 in the Review indicated that the importance of leafiness in tropical swards was probably a reflection of the relatively low leaf density in the surface stratum compared with temperate swards. As there is usually a greater contrast in the quality of leaf and stem on tropical than on temperate swards, the drive to select green leaf was likely to have been higher on tropical swards.

With regards to the relative importance of height and density, both the cage trials and the work of Black and Kenney (1984) have clearly shown that both variables determine bite weight, but there may be several reasons why previous trials have failed to detect this.

First of all, there has been some degree of confounding of sward height and density, and often digestibility, in virtually all of the previous work. This would obscure the true causative variables, and for example whilst Stobbs (1973a, 1975b), Chacon and Stobbs (1976) and Hendricksen and Minson (1980) considered that the main variables influencing bite weight on their tropical swards were bulk density and leaf content, the data which they quoted also indicated that surface height might have had an effect.

Secondly, the quality and applicability of certain sward measurements were poor in the early experiments, for example the use of the estimate of the mean bulk density of the whole sward rather than of the grazed stratum.

Thirdly, if there was only a small range of variation in either height or density within a particular trial, it would be difficult to detect its effect on bite weight, particularly if there was a large range of variation in the other sward variable.

The grazing cage technique

The contrasting approaches taken in the two current experiments each had their advantages and drawbacks. Only in Experiment 1 were bite rate, grazing time and daily herbage intake measured, allowing long-term grazing responses to be assessed in addition to the short-term, bite weight, responses. Patterns of behaviour as swards were defoliated were established, and the importance of bite weight in determining daily intake, both within and between swards, was highlighted. However, in terms of defining responses in bite weight to changes in sward height and density, the cage trials were clearly much more successful than the more conventional, large plot grazing trials. Indeed, it was only possible to show conclusively within a particular experiment that both sward variables determined bite weight when the experimental conditions were tightly controlled, as in the cage trials and the artificial pasture trials run by Black and Kenney (1984). To date, only the cage trials have been able to establish that on natural swards the effects of surface height and grazed stratum bulk density on bite weight are independent and additive.

The new technique of using grazing cages had several practical advantages over the more conventional approach. The cages allowed observers to work close to the sheep and make detailed measurements. Bite depth, bite weight and the grazed stratum bulk density were measured more directly and probably more accurately on the small uniform cage patches than on the much more extensive and variable plots used in Experiment 1. Direct estimates of true bite area and volume could only be obtained in the cage trials, and this allowed the complete set of bite measurements to be related to the sward characteristics of the specific patches of vegetation grazed. The complications of trampling and fouling of the experimental herbage were avoided, and the dynamic component of the bite responses would have been minimal within any particular trial.

Compared with the conventional type of trial, the cage technique used far fewer resources and produced results more quickly. Although oesophageal fistulated animals were used in both experiments, surgically modified animals would not be required for the cage technique if turves rather than small areas of a plot were used to provide the experimental herbage. Bite weight could be estimated directly from the change in turf weight during sampling (although in extreme environmental conditions the gain or loss of water from the turf during sampling might also have to be taken into account). Whatever the methodology, the animals used in grazing cages must be reasonably tame.

The cage technique has considerable potential for further investigation of a number of aspects of grazing responses. Additional trials are required, on a more comprehensive range of swards, to confirm whether sward features such as dead material, or pseudostem in a vegetative sward, do limit bite depth. Indications that bite area responds to changes in herbage mass, surface height and the population density of grazed plant units need to be verified, and the summit force per bite theory could probably be most easily investigated using grazing cages. Grazing mechanics could be examined in some detail by allowing sheep to graze turves on a force platform, as Bignall (1984) did for geese. The forces associated with severing herbage from contrasting swards could be related to measurements of the mechanical properties (stiffness and tensile strength) of the leaves and stems and the number of each type of plant unit severed at a bite.

In view of the apparent importance of diet digestibility in determining bite depth and bite weight in Experiment 1, it would be interesting to measure this variable in further cage trials. This would establish whether, under controlled conditions, sward quality had any effect on bite responses over and above the effects of sward canopy structure.

Bite rate was not measured in the cage trials either. It was considered that the sheep were allowed to graze for too short a time to establish a steady bite rate, but these fears might not have been justified. Black and Kenney (1984) allowed sheep to graze for only 30 seconds while bite rate was recorded, and the bite rate responses obtained did conform with the trends found in previous work. If bite rate was measured in future work with grazing cages, this would allow responses in rate of intake to be identified in addition to those for bite weight.

As far as could be ascertained in Experiment 1, bite depth responses in cattle were broadly similar to those for sheep, although there did appear to be differences in bite depth between the two species on certain swards. In order to clarify to what extent responses in bite depth and the other bite measurements vary with mouth size and method of herbage prehension, detailed grazing observations are required on different animal species, and on different breeds within a species. The cage technique would be well suited for such a study, and for addressing the question of whether there is any modifying effect on bite dimensions, bite weight and bite rate due to differences in animal factors such as physiological state, body condition and hunger.

Conclusions

It was concluded from the current investigation that bite weight in grazing sheep was influenced by both sward surface height and grazed stratum bulk density, and that these effects were independent and additive and the joint response surface planar. The surface height effect appeared to be mediated predominantly via bite depth, whilst density acted on bite weight directly. As bite weight was the main determinant of daily herbage intake, both of these grazing responses would increase as swards became taller and had a greater density in the grazed stratum.

Consequently, the results presented here indicate a serious challenge for the plant breeder; to produce swards which are comparatively tall and dense in order to stimulate a high intake in the grazing animal, and yet to maintain suitable agronomic characteristics such as leafiness and resistance to trampling in order to boost production from grassland.

APPENDIX E1

Appendix Tables E1.1 to E1.11 and Appendix Figure E1.1

Appendix Table E1.1

The mean herbage mass (kg OM ha^{-1}) of each sward grazed down over two subperiods (1983) or four subperiods (1984)

Year and month	Grazing trial	Crop	Plot	Subperiod 1	Subperiod 2			Crop mean
1983								
June	I	barley	L	1860	1160			
			M	2150	1160			2040
			H	3400	2540			
July	II	red fescue	L	890	510			
			M	880	530			840
			H	1310	920			
Sept.	III	am. PRG	L	990	850			
			M	1540	1140			1360
			H	1950	1660			
Sept.	III	rye	L	1430	1050			
			M	1520	1250			1410
			H	1790	1440			
Oct.	IV	PRG	L	1590	1190			
			M	2810	1970			2140
			H	3060	2220			
1984				1	2	3	4	
July	I	oats	L	1200	940	680	420	
			M	1760	1500	1240	980	1210
			H	1860	1600	1330	1060	
Aug.	II	am. PRG	L	2220	2080	1940	1800	
			M	2570	2350	2130	1900	2140
			H	2500	2280	2070	1850	
Aug.	II	timothy	L	1330	1070	810	550	
			M	1950	1500	1050	590	1220
			H	2100	1660	1210	760	
Sept.	III	*Agrostis*	L	2060	1820	1570	1320	
			M	1150	1010	880	740	1390
			H	1730	1600	1480	1350	
Sept.	III	PRG1	T	3000	2730	2450	2180	2260
			B	2210	2020	1830	1640	
Oct.	IV	barley	L	250	220	190	160	
			H	820	650	470	300	380
Oct.	IV	PRG4	S	1610	1510	1400	1300	
			Lg	2930	2620	2310	2010	1960

Appendix Table E1.2

The proportion of gramineous material in the stratum grazed by sheep grazing down each sward over two subperiods (1983) or four subperiods (1984)

Year and month–	Grazing trial	Crop	Plot	Subperiod 1	Subperiod 2		
1983							
June	I	barley	L	0.99	0.98		
			M	0.97	0.98		
			H	1.00	1.00		
July	II	red fescue	L	0.83	0.87		
			M	>0.99	0.98		
			H	0.99	0.97		
Sept.	III	am. PRG	L	0.98	0.98		
			M	>0.99	>0.99		
			H	>0.99	>0.99		
Sept.	III	rye	L	1.00	1.00		
			M	1.00	1.00		
			H	1.00	1.00		
Oct.	IV	PRG	L	1.00	1.00		
			M	0.99	0.99		
			H	1.00	1.00		
1984				1	2	3	4
July	I	oats	L	0.89	0.78	0.68	0.70
			M	0.94	0.96	0.97	0.97
			H	0.97	0.95	0.87	0.75
Aug.	II	am. PRG	L	0.87	0.89	0.90	0.91
			M	>0.99	0.99	0.99	0.99
			H	0.98	0.98	0.98	0.99
Aug.	II	timothy	L	0.92	0.82	0.64	0.61
			M	0.87	0.86	0.82	0.80
			H	0.93	0.92	0.92	0.92
Sept.	III	*Agrostis*	L	1.00	1.00	1.00	1.00
			M	0.99	0.96	0.96	0.98
			H	0.98	0.99	0.98	0.98
Sept.	III	PRG1	T	1.00	>0.99	>0.99	1.00
			B	1.00	>0.99	>0.99	>0.99
Oct.	IV	barley	L	>0.99	0.98	0.97	0.98
			H	>0.99	0.99	0.99	0.98
Oct.	IV	PRG4	S	1.00	1.00	1.00	1.00
			Lg	1.00	1.00	1.00	1.00

Appendix Table E1.3

The proportion of green (live) material in the gramineous fraction of the stratum grazed by sheep grazing down each sward over two subperiods (1983) or four subperiods (1984)

Year and month	Grazing trial	Crop	Plot	Subperiod 1		Subperiod 2	
1983							
June	I	barley	L	0.99		0.97	
			M	0.97		0.88	
			H	>0.99		0.99	
July	II	red fescue	L	0.98		0.97	
			M	0.98		0.96	
			H	0.97		0.92	
Sept.	III	am. PRG	L	0.99		0.99	
			M	0.97		0.95	
			H	0.97		0.95	
Sept.	III	rye	L	0.90		0.84	
			M	0.94		0.89	
			H	0.85		0.80	
Oct.	IV	PRG	L	0.94		0.92	
			M	0.90		0.83	
			H	0.86		0.80	
1984				1	2	3	4
July	I	oats	L	0.99	0.99	0.97	0.94
			M	0.99	0.99	0.99	0.98
			H	0.97	0.97	0.97	0.96
Aug.	II	am. PRG	L	0.97	0.95	0.93	0.92
			M	0.94	0.92	0.91	0.89
			H	0.93	0.89	0.86	0.85
Aug.	II	timothy	L	0.97	0.98	0.98	0.97
			M	0.94	0.92	0.87	0.86
			H	0.91	0.89	0.87	0.84
Sept.	III	*Agrostis*	L	0.95	0.90	0.87	0.85
			M	0.99	0.98	0.97	0.93
			H	0.97	0.96	0.94	0.92
Sept.	III	PRG1	T	0.98	0.98	0.97	0.96
			B	0.97	0.96	0.95	0.95
Oct.	IV	barley	L	0.92	0.91	0.90	0.86
			H	0.84	0.83	0.80	0.83
Oct.	IV	PRG4	S	0.94	0.88	0.84	0.80
			Lg	0.96	0.92	0.89	0.87

Appendix Table E1.4

The proportion of leaf in the gramineous fraction of the stratum grazed by sheep grazing down each sward over two subperiods (1983) or four subperiods (1984)

Year and month	Grazing trial	Crop	Plot	Subperiod 1	2	3	4	Crop mean
1983								
June	I	barley	L	0.77	0.62			
			M	0.80	0.60			0.65
			H	0.58	0.51			
July	II	red fescue	L	0.73	0.67			
			M	0.93	0.76			0.79
			H	0.91	0.71			
Sept.	III	am. PRG	L	0.96	0.93			
			M	0.87	0.68			0.87
			H	0.94	0.84			
Sept.	III	rye	L	0.91	0.81			
			M	0.93	0.83			0.86
			H	0.90	0.79			
Oct.	IV	PRG	L	0.97	0.93			
			M	0.94	0.86			0.90
			H	0.92	0.78			
1984				1	2	3	4	
July	I	oats	L	0.71	0.53	0.30	0.29	
			M	0.65	0.47	0.30	0.28	0.46
			H	0.69	0.58	0.38	0.30	
Aug.	II	am. PRG	L	0.76	0.47	0.32	0.28	
			M	0.72	0.59	0.48	0.40	0.58
			H	0.84	0.77	0.69	0.61	
Aug.	II	timothy	L	0.69	0.71	0.75	0.70	
			M	0.64	0.64	0.62	0.56	0.62
			H	0.66	0.57	0.48	0.47	
Sept.	III	*Agrostis*	L	0.76	0.65	0.58	0.58	
			M	0.89	0.82	0.76	0.71	0.74
			H	0.89	0.81	0.74	0.71	
Sept.	III	PRG1	T	0.95	0.92	0.91	0.91	0.93
			B	0.97	0.95	0.93	0.90	
Oct.	IV	barley	L	0.66	0.58	0.48	0.44	0.51
			H	0.73	0.57	0.32	0.26	
Oct.	IV	PRG4	S	0.89	0.82	0.76	0.71	0.81
			Lg	0.94	0.90	0.78	0.67	
S.e. of crop means[a] and significance of differences between crops				1983				0.018***
				1984 0.011, 0.010 or				0.009[b]***

[a] The s.e. presented is an average value; when there are large differences in the size of table entries it may not be appropriate to each entry.

[b] When comparing two crops each with two plots, a crop with two plots with a crop with three plots, and two crops each with three plots, respectively.

Appendix Table E1.5

The bulk density (mg OM cm^{-3}) of gramineous material in the stratum grazed by sheep grazing down each sward over two subperiods (1983) or four subperiods (1984)

Year and month	Grazing trial	Crop	Plot	Subperiod 1	2	3	4	Crop mean
1983								
June	I	barley	L	0.46	0.45			
			M	0.47	0.65			0.54
			H	0.59	0.59			
July	II	red fescue	L	1.11	0.90			
			M	0.60	0.99			0.93
			H	0.65	1.32			
Sept.	III	am. PRG	L	0.39	0.48			
			M	0.86	1.32			0.81
			H	0.88	0.95			
Sept.	III	rye	L	0.59	0.57			
			M	0.45	0.54			0.62
			H	0.79	0.77			
Oct.	IV	PRG	L	0.65	0.62			
			M	1.03	1.16			1.03
			H	1.28	1.45			
1984				1	2	3	4	
July	I	oats	L	0.28	0.29	0.32	0.37	
			M	0.42	0.48	0.53	0.56	0.43
			H	0.56	0.53	0.45	0.36	
Aug.	II	am. PRG	L	0.98	1.03	1.09	1.17	
			M	1.28	1.35	1.33	1.31	1.27
			H	1.43	1.48	1.44	1.31	
Aug.	II	timothy	L	0.49	0.58	0.13	0.11	
			M	1.50	0.95	0.64	0.56	0.76
			H	1.48	1.12	0.77	0.82	
Sept.	III	*Agrostis*	L	1.05	1.08	1.41	1.35	
			M	0.48	0.52	0.62	0.74	0.91
			H	0.84	0.91	0.94	0.97	
Sept.	III	PRG1	T	1.64	1.81	1.79	1.66	1.61
			B	1.38	1.54	1.55	1.53	
Oct.	IV	barley	L	0.06	0.10	0.13	0.13	0.15
			H	0.18	0.17	0.18	0.27	
Oct.	IV	PRG4	S	0.92	1.04	1.16	1.40	1.20
			Lg	1.08	1.14	1.19	1.65	
S.e. of crop means[a] and significance of differences between crops				1983				0.068**
				1984 0.026, 0.024 or				0.021[b]***

[a] The s.e. presented is an average value; when there are large differences in the size of table entries it may not be appropriate to each entry.

[b] When comparing two crops each with two plots, a crop with two plots with a crop with three plots, and two crops each with three plots, respectively.

Appendix Table E1.6

The bulk density (mg OM cm^{-3}) of gramineous green (live) material in the stratum grazed by sheep grazing down each sward over two subperiods (1983) or four subperiods (1984)

Year and month	Grazing trial	Crop	Plot	Subperiod 1	Subperiod 2			Crop mean
1983								
June	I	barley	L	0.46	0.44			
			M	0.46	0.58			0.52
			H	0.59	0.59			
July	II	red fescue	L	1.09	0.87			
			M	0.59	0.95			0.89
			H	0.63	1.21			
Sept.	III	am. PRG	L	0.39	0.48			
			M	0.83	1.26			0.78
			H	0.85	0.90			
Sept.	III	rye	L	0.53	0.47			
			M	0.42	0.48			0.53
			H	0.67	0.62			
Oct.	IV	PRG	L	0.61	0.57			
			M	0.92	0.97			0.89
			H	1.10	1.16			
1984				Subperiod 1	Subperiod 2	Subperiod 3	Subperiod 4	
July	I	oats	L	0.28	0.29	0.31	0.35	
			M	0.41	0.47	0.53	0.55	0.42
			H	0.54	0.52	0.44	0.34	
Aug.	II	am. PRG	L	0.95	0.98	1.02	1.07	
			M	1.20	1.25	1.21	1.17	1.16
			H	1.33	1.32	1.24	1.12	
Aug.	II	timothy	L	0.48	0.56	0.13	0.11	
			M	1.41	0.88	0.56	0.48	0.69
			H	1.34	1.00	0.67	0.69	
Sept.	III	*Agrostis*	L	1.00	0.98	1.23	1.14	
			M	0.47	0.51	0.60	0.69	0.84
			H	0.82	0.87	0.89	0.89	
Sept.	III	PRG1	T	1.61	1.77	1.74	1.60	1.56
			B	1.33	1.47	1.47	1.45	
Oct.	IV	barley	L	0.06	0.09	0.12	0.11	0.13
			H	0.15	0.14	0.14	0.22	
Oct.	IV	PRG4	S	0.86	0.92	0.97	1.12	1.06
			Lg	1.04	1.05	1.05	1.43	

S.e. of crop means[a] and significance of differences between crops: 1983 0.062 **; 1984 0.024, 0.022 or 0.019[b] ***

[a] The s.e. presented is an average value; when there are large differences in the size of table entries it may not be appropriate to each entry.

[b] When comparing two crops each with two plots, a crop with two plots with a crop with three plots, and two crops each with three plots, respectively.

Appendix Table E1.7

The bulk density (mg OM cm^{-3}) of gramineous leaf in the stratum grazed by sheep grazing down each sward over two subperiods (1983) or four subperiods (1984)

Year and month	Grazing trial	Crop	Plot	Subperiod 1	2	3	4	Crop mean
1983								
June	I	barley	L	0.36	0.28			0.34
			M	0.38	0.39			
			H	0.34	0.30			
July	II	red fescue	L	0.81	0.60			0.71
			M	0.56	0.75			
			H	0.59	0.94			
Sept.	III	am. PRG	L	0.37	0.45			0.68
			M	0.75	0.90			
			H	0.83	0.79			
Sept.	III	rye	L	0.54	0.46			0.53
			M	0.42	0.45			
			H	0.71	0.61			
Oct.	IV	PRG	L	0.63	0.58			0.92
			M	0.97	1.00			
			H	1.18	1.13			
1984				1	2	3	4	
July	I	oats	L	0.20	0.16	0.10	0.11	0.20
			M	0.27	0.22	0.16	0.15	
			H	0.38	0.31	0.17	0.11	
Aug.	II	am. PRG	L	0.74	0.48	0.34	0.33	0.74
			M	0.92	0.80	0.64	0.52	
			H	1.21	1.14	0.99	0.80	
Aug.	II	timothy	L	0.34	0.41	0.10	0.08	0.46
			M	0.95	0.60	0.39	0.31	
			H	0.97	0.64	0.37	0.39	
Sept.	III	*Agrostis*	L	0.81	0.70	0.82	0.79	0.65
			M	0.43	0.43	0.47	0.53	
			H	0.75	0.73	0.70	0.68	
Sept.	III	PRG1	T	1.55	1.67	1.64	1.51	1.50
			B	1.33	1.47	1.44	1.38	
Oct.	IV	barley	L	0.04	0.06	0.06	0.06	0.07
			H	0.13	0.10	0.06	0.07	
Oct.	IV	PRG4	S	0.82	0.86	0.88	1.00	0.96
			Lg	1.02	1.03	0.93	1.10	

S.e. of crop means[a] and significance of differences between crops: 1983 0.041***; 1984 0.020, 0.018 or 0.016[b]***

[a] The s.e. presented is an average value; when there are large differences in the size of table entries it may not be appropriate to each entry.

[b] When comparing two crops each with two plots, a crop with two plots with a crop with three plots, and two crops each with three plots, respectively.

Appendix Table E1.8

The mean live weight (kg) of the non-fistulated sheep on each plot at the start of a trial

Year and month	Grazing trial	Crop	Plot L	Plot M	Plot H
1983					
June	I	barley	33.7	31.9	31.9
July	II	red fescue	37.2	38.1	35.8
Sept.	III	am. PRG	42.4	43.4	43.2
		rye	43.6	44.7	42.7
Oct.	IV	PRG	45.5	44.7	47.9
1984					
July	I	oats	42.0	41.7	42.5
Aug.	II	am. PRG	43.4	43.7	44.0
		timothy	43.4	44.7	43.3
Sept.	III	Agrostis	46.2	45.4	47.0
		PRG1		T: 49.0 B: 47.8	
Oct.	IV	barley	48.7		48.8
		PRG4		S: 48.1 Lg: 48.2	

Appendix Table E1.9

The estimated bite volume (cm^3) of sheep grazing down each sward over two subperiods (1983) or four subperiods (1984)

Year and month	Grazing trial	Crop	Plot	Subperiod 1	Subperiod 2	Subperiod 3	Subperiod 4	Crop mean
1983								
June	I	barley	L	116	97			
			M	119	51			94
			H	93	86			
July	II	red fescue	L	37	25			
			M	126	32			54
			H	82	24			
Sept.	III	am. PRG	L	135	50			
			M	52	22			53
			H	36	24			
Sept.	III	rye	L	121	114			
			M	144	90			100
			H	78	56			
Oct.	IV	PRG	L	75	40			
			M	44	17			40
			H	40	20			
1984				1	2	3	4	
July	I	oats	L	431	165	112	103	
			M	170	112	87	86	139
			H	148	90	87	75	
Aug.	II	am. PRG	L	94	67	48	34	
			M	71	46	31	25	50
			H	76	41	34	30	
Aug.	II	timothy	L	141	73	265	429	
			M	35	63	101	93	115
			H	39	35	57	50	
Sept.	III	*Agrostis*	L	53	32	30	24	
			M	135	83	58	36	55
			H	82	50	42	32	
Sept.	III	PRG1	T	26	25	16	18	24
			B	38	27	21	18	
Oct.	IV	barley	L	1083	496	330	235	436
			H	561	359	221	205	
Oct.	IV	PRG4	S	32	22	13	11	26
			Lg	42	33	28	25	

Appendix Table E1.10

The estimated bite area (cm^2) of sheep grazing down each sward over two subperiods (1983) or four subperiods (1984)

Year and month	Grazing trial	Crop	Plot	Subperiod				Crop mean
				1	2			
1983								
June	I	barley	L	13.9	40.5			
			M	15.6	23.1			19.6
			H	11.1	13.3			
July	II	red fescue	L	15.4	12.7			
			M	31.5	19.1			16.4
			H	14.9	4.8			
Sept.	III	am. PRG	L	35.4	29.5			
			M	10.4	5.2			15.6
			H	6.9	6.0			
Sept.	III	rye	L	40.2	71.5			
			M	41.2	37.4			44.3
			H	35.5	39.9			
Oct.	IV	PRG	L	14.4	9.0			
			M	10.1	3.8			8.9
			H	10.0	5.9			
1984				1	2	3	4	
July	I	oats	L	37.5	48.6	93.5	85.8	
			M	13.0	16.0	21.7	34.6	34.3
			H	11.4	15.2	15.2	19.7	
Aug.	II	am. PRG	L	16.5	11.2	7.8	13.8	
			M	11.0	8.2	5.4	5.0	11.3
			H	13.3	14.1	10.8	18.8	
Aug.	II	timothy	L	22.4	18.2	106.1	357.9	
			M	6.9	48.5	84.2	77.3	66.4
			H	6.2	5.2	22.7	41.8	
Sept.	III	*Agrostis*	L	10.0	5.8	5.5	4.6	
			M	29.4	24.4	23.3	25.7	13.9
			H	15.4	9.4	7.6	5.9	
Sept.	III	PRG1	T	4.6	4.2	3.2	3.2	4.9
			B	12.7	4.7	3.7	3.1	
Oct.	IV	barley	L	116.5	77.5	61.2	93.9	71.8
			H	44.8	46.6	40.8	93.1	
Oct.	IV	PRG4	S	5.8	8.8	7.7	9.0	9.2
			Lg	7.7	6.2	18.6	10.1	

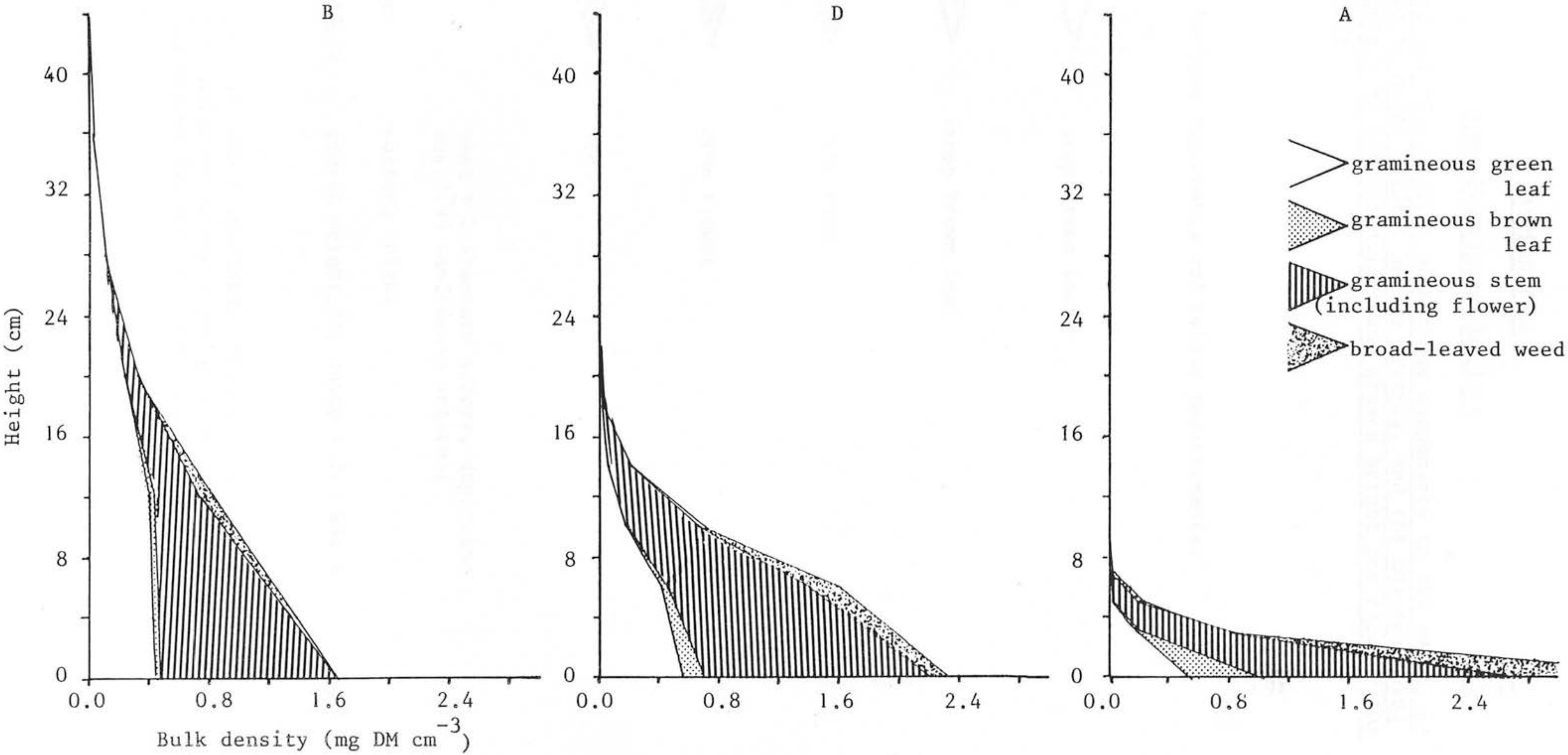
Appendix Table E1.11

Daylength (h daylight d^{-1}) on the central day of each intake subperiod of each grazing trial in 1983 and 1984

Year and month	Grazing Trial	Crop	Subperiod 1		Subperiod 2	
1983						
June	I	barley	17.53		17.43	
July	II	red fescue	16.42		16.23	
Sept.	III	am. PRG / rye	12.78		12.55	
Oct.	IV	PRG	11.25		10.93	
1984			1	2	3	4
July	I	oats	17.05	16.95	16.87	16.77
Aug.	II	am. PRG / timothy	15.38	15.23	15.10	14.98
Sept.	III	Agrostis / PRG1	13.33	13.18	13.03	12.87
Oct.	IV	barley / PRG4	10.50	10.33	10.18	10.05

Appendix Figure E1.1

The herbage composition of the oats M sward profile, measured by stratified clip before (B), during (D) and after (A) grazing

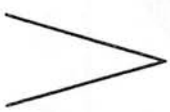


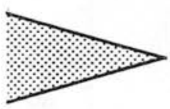
APPENDIX E2

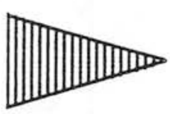
Appendix Figures E2.1a-q

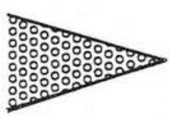
The vertical distribution of herbage components in the sward, as measured by point quadrat before grazing, and the corresponding measurements of surface height and grazed height for each of the four sheep

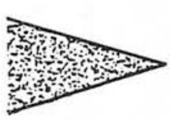
Key to herbage components and height measurements:

 crop green leaf

 crop brown leaf

 crop stem

 crop flower

 weed

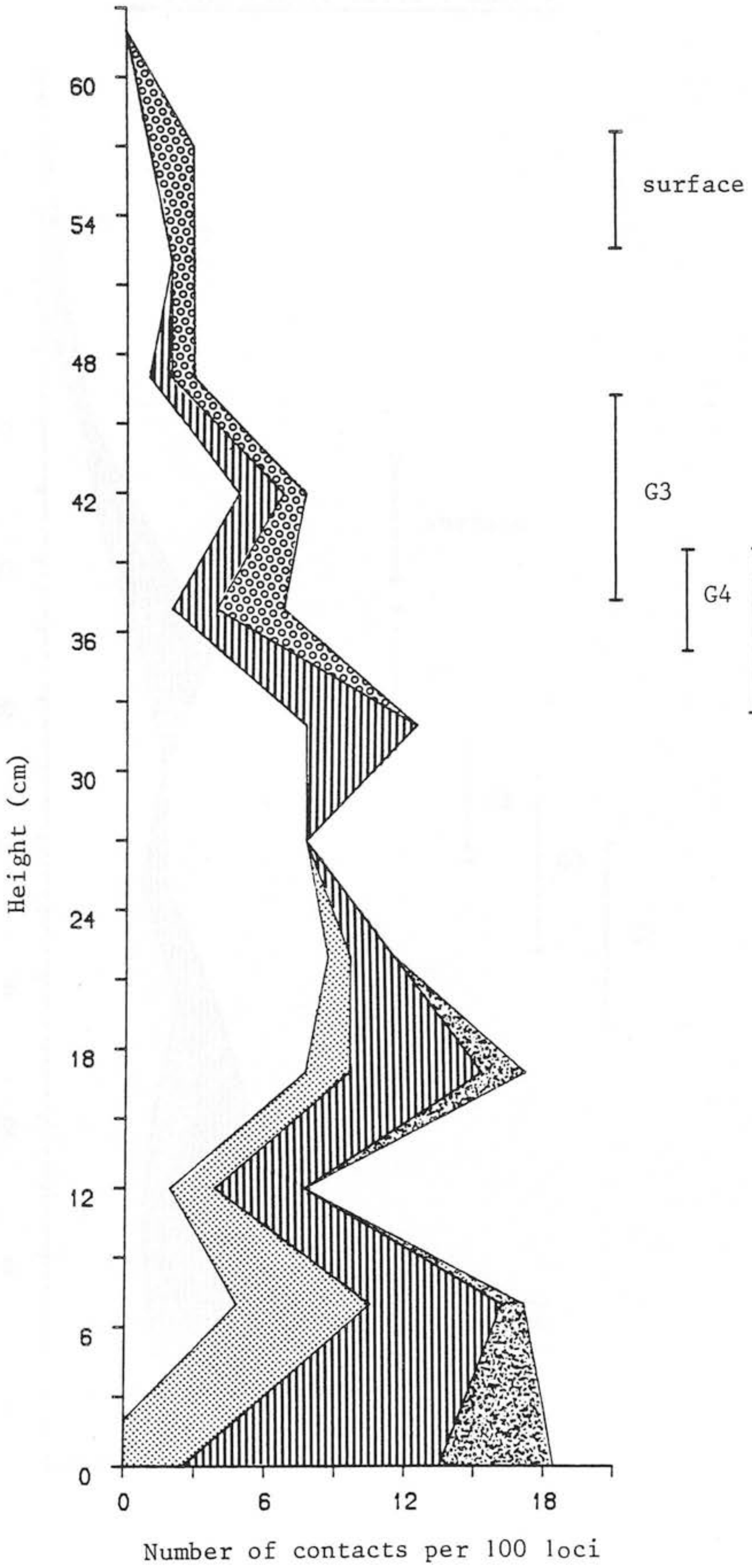
 mean ± 2 standard errors, depicting the 0.95 confidence interval

surface — surface height

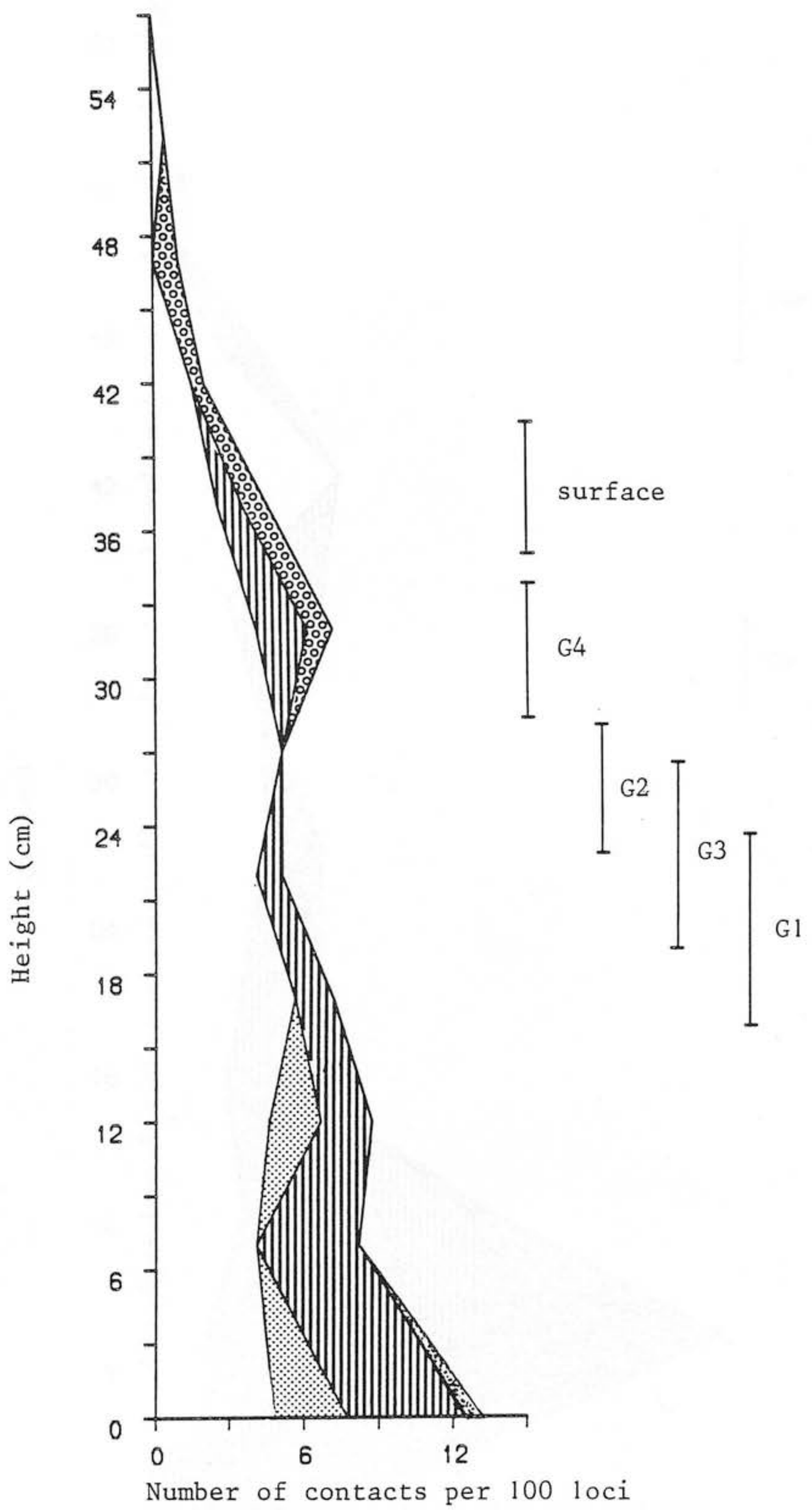
G1,G2,G3,G4 — grazed height for sheep 1,2,3 and 4

Notes: All data are unsmoothed. Occasionally, data for a particular sheep are missing if it did not graze. The scales for the two axes vary between diagrams.

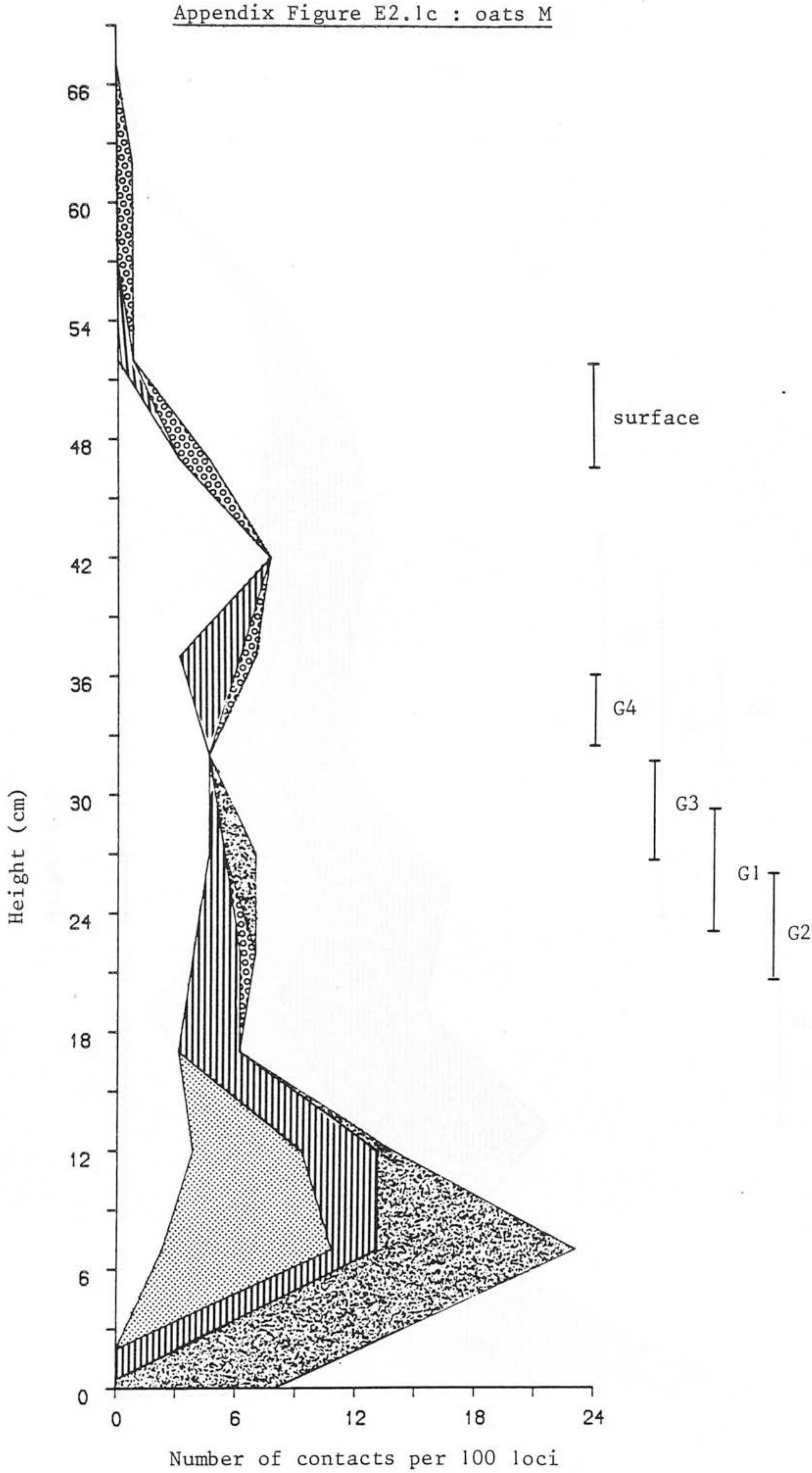
Appendix Figure E2.1a : oats H



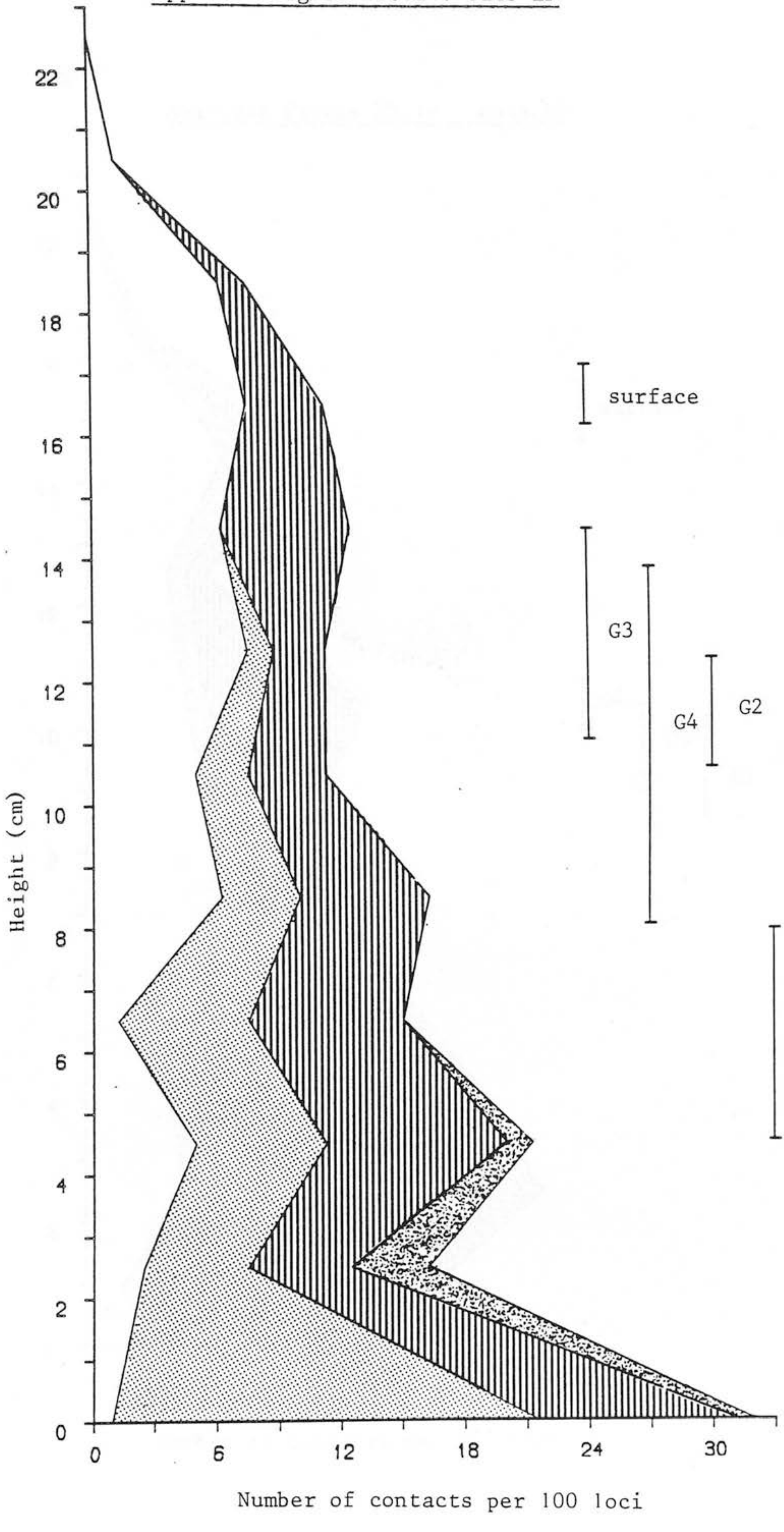
Appendix Figure E2.1b : oats L



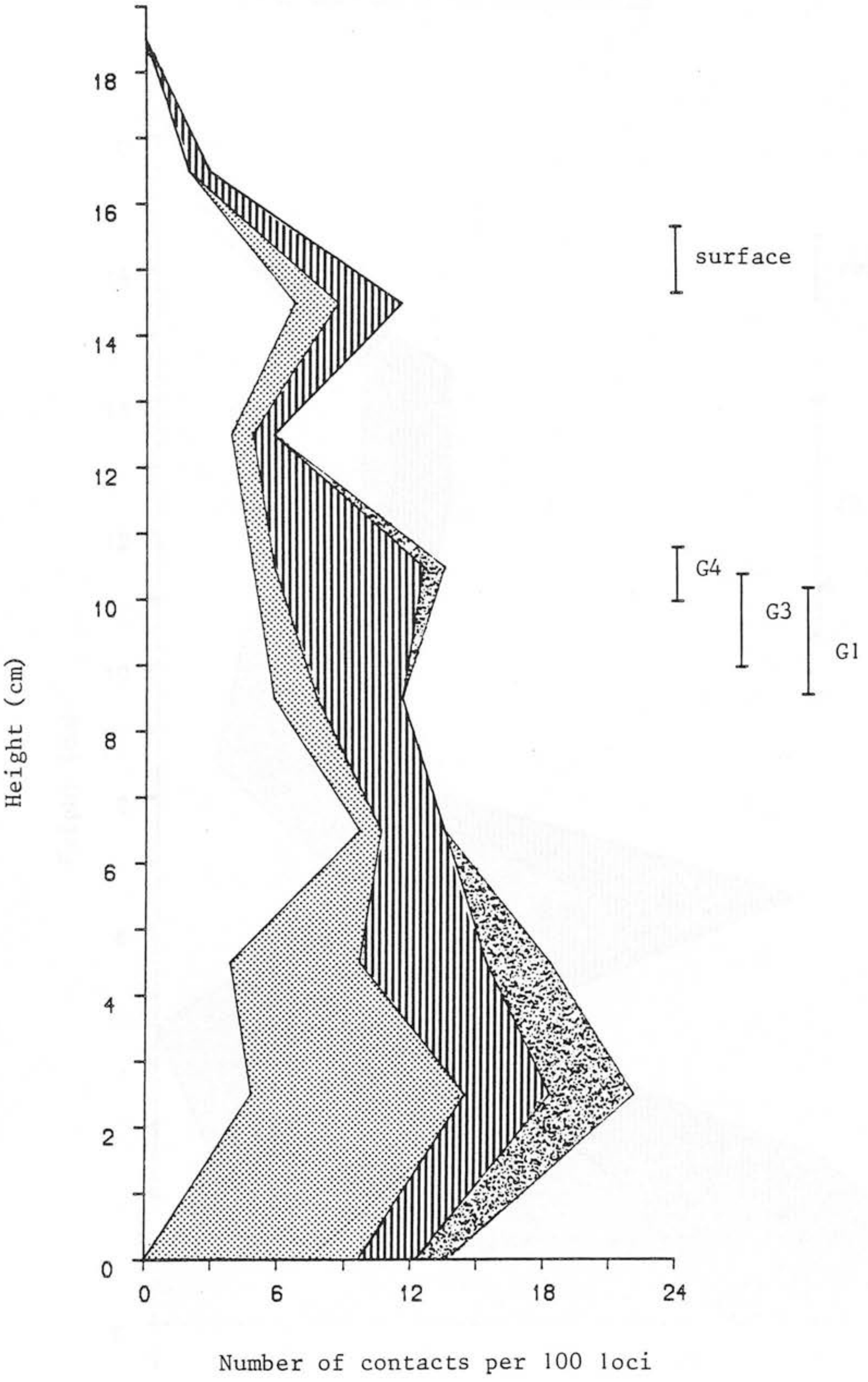
Appendix Figure E2.1c : oats M



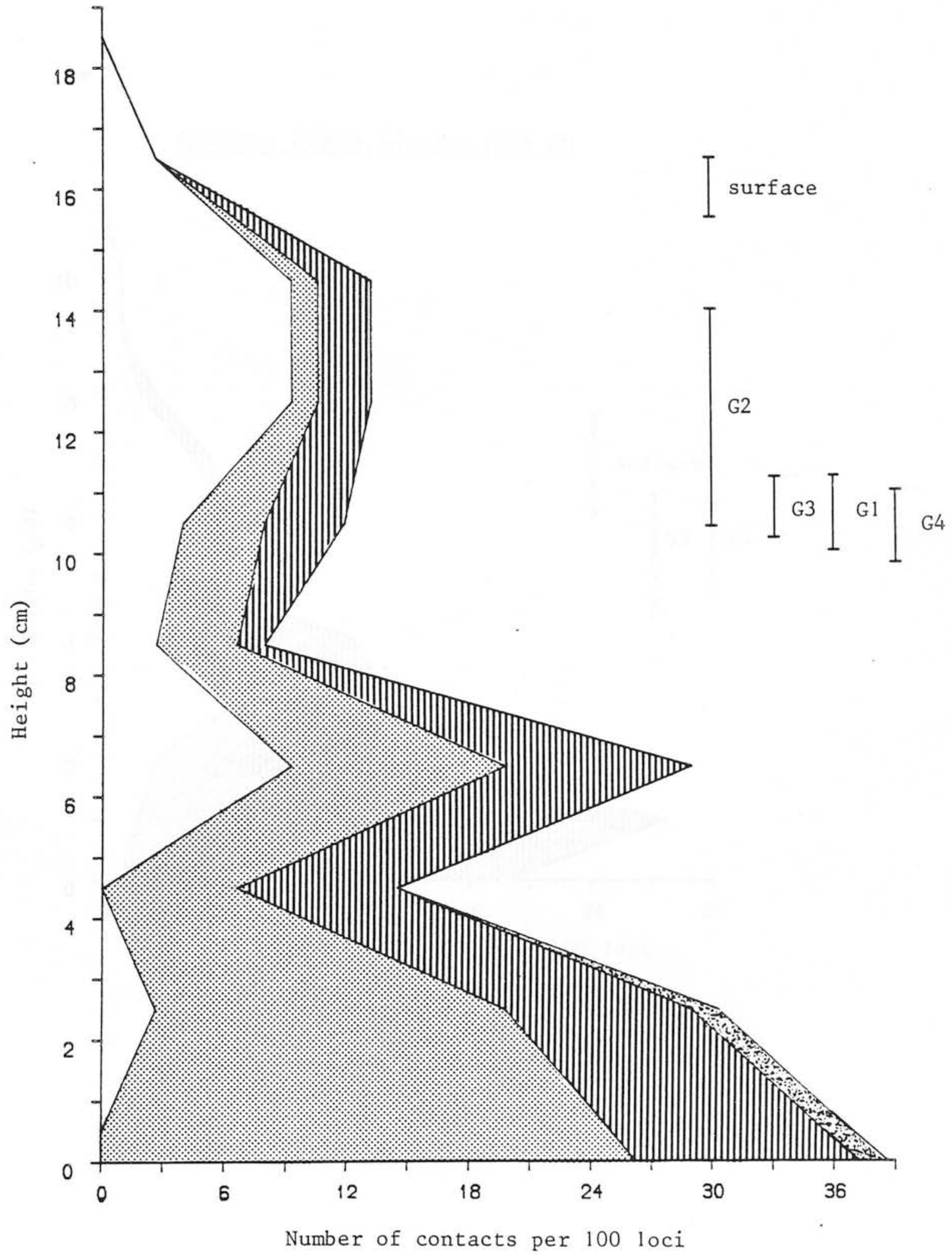
Appendix Figure E2.1d : oats LP



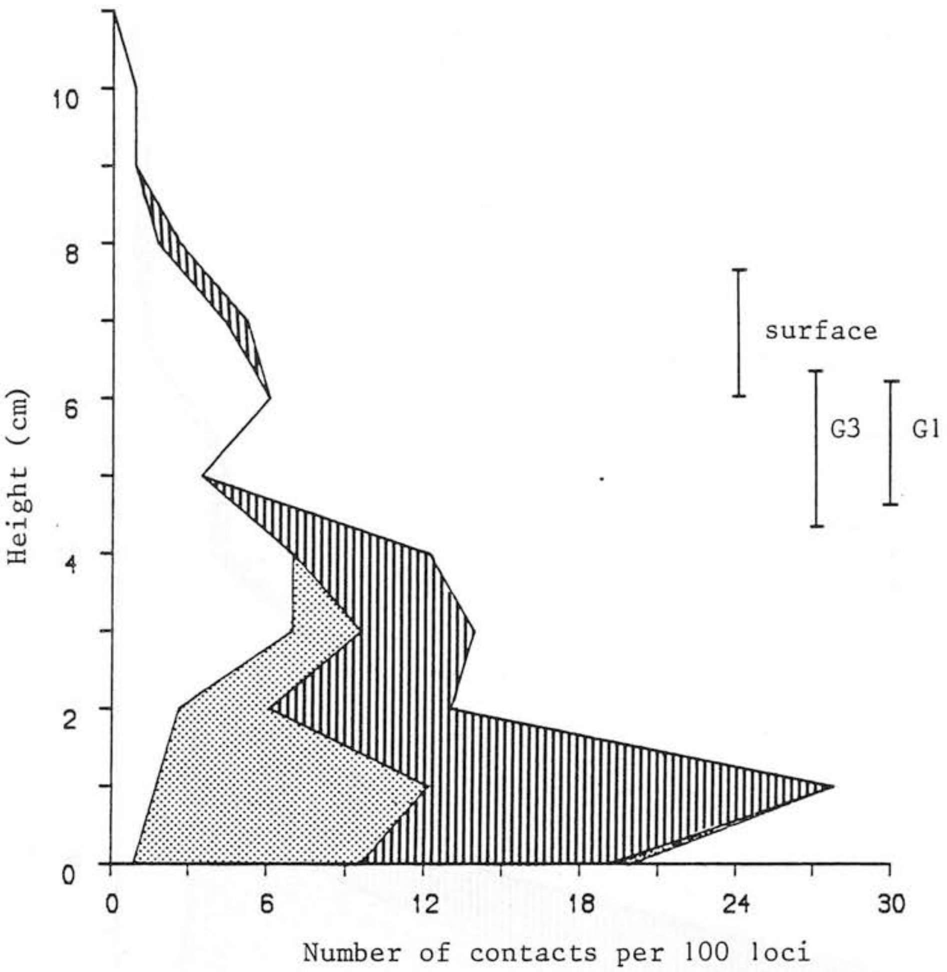
Appendix Figure E2.1e : oats MP



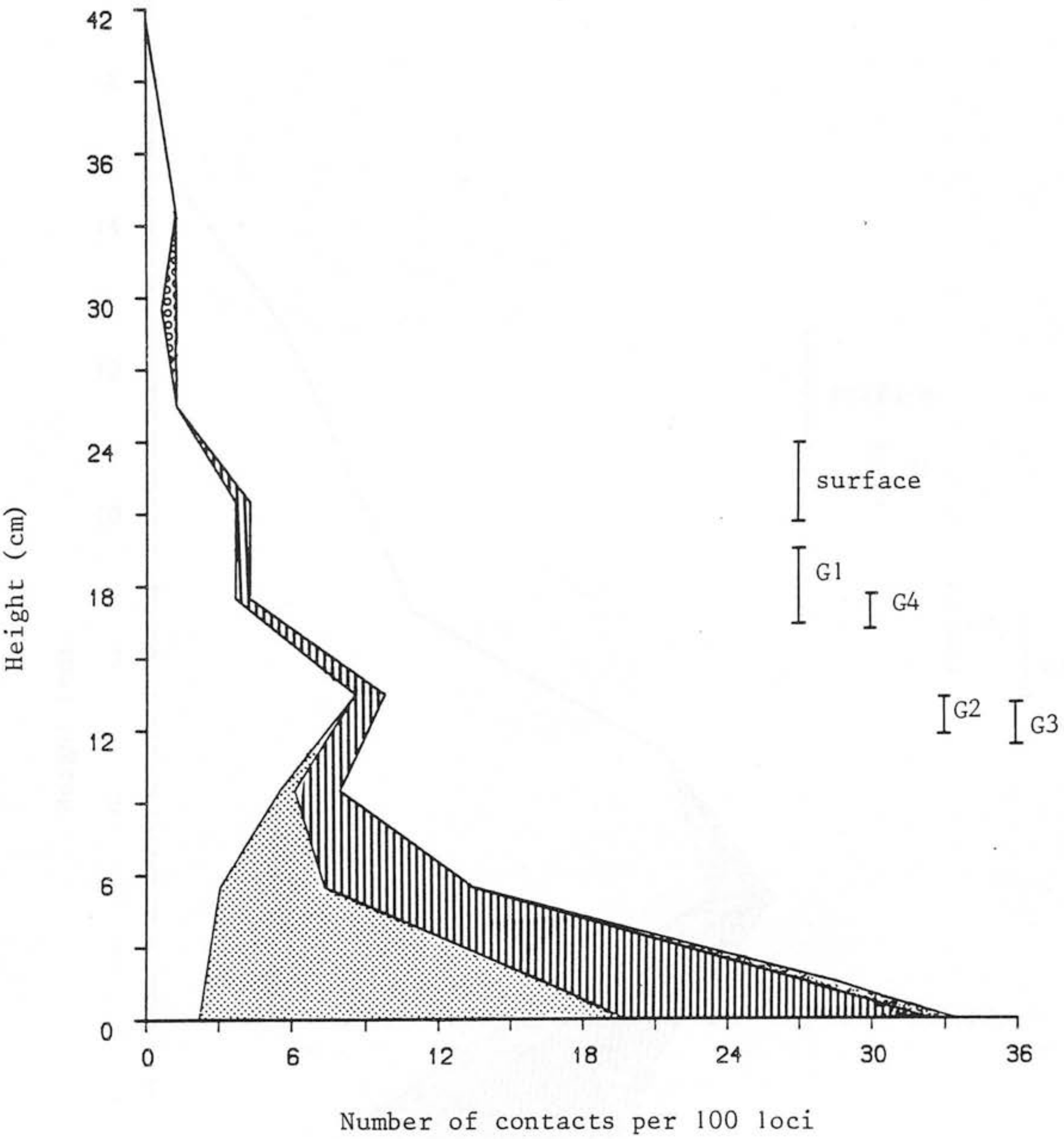
Appendix Figure E2.1f : oats HP



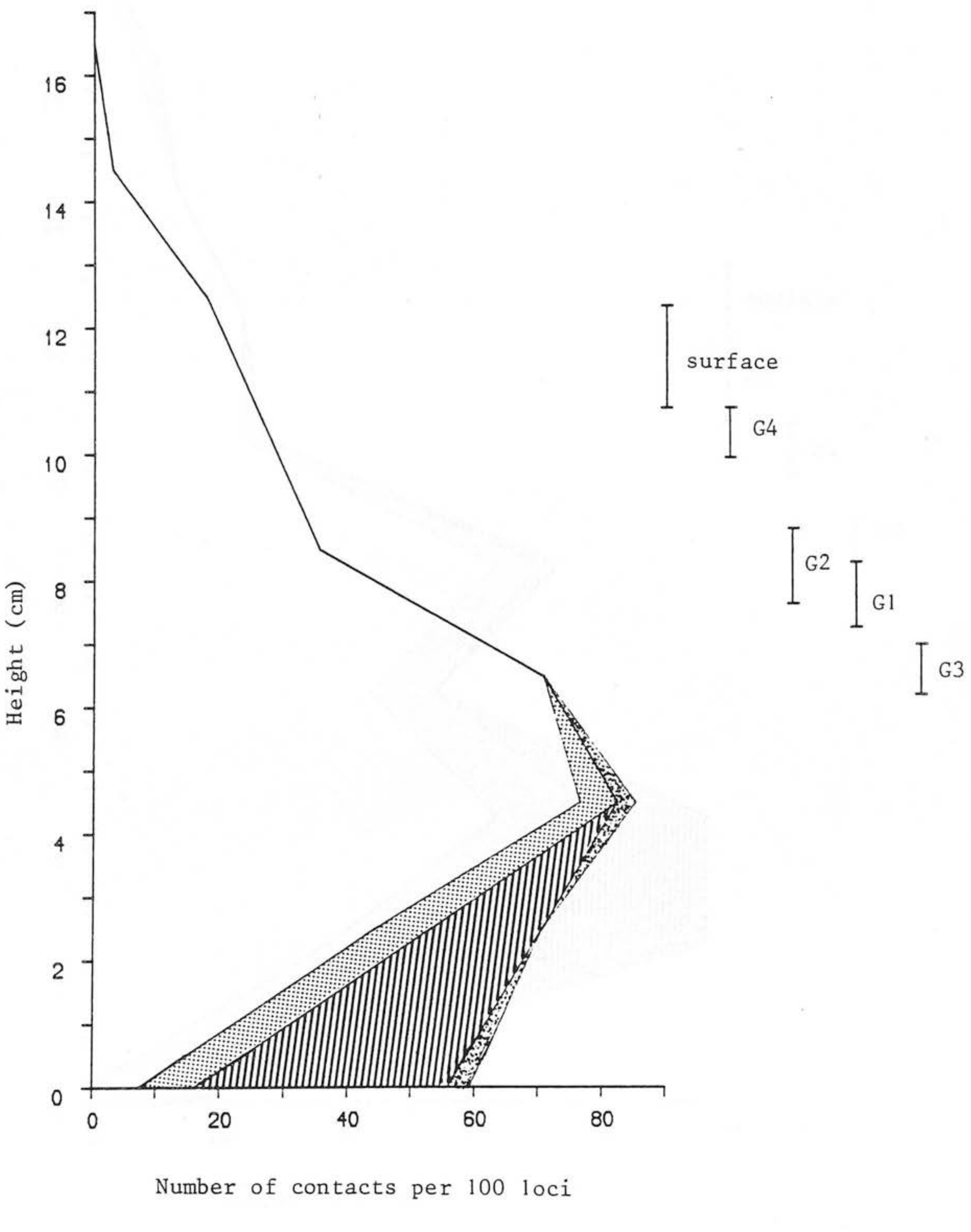
Appendix Figure E2.1g : oats MG



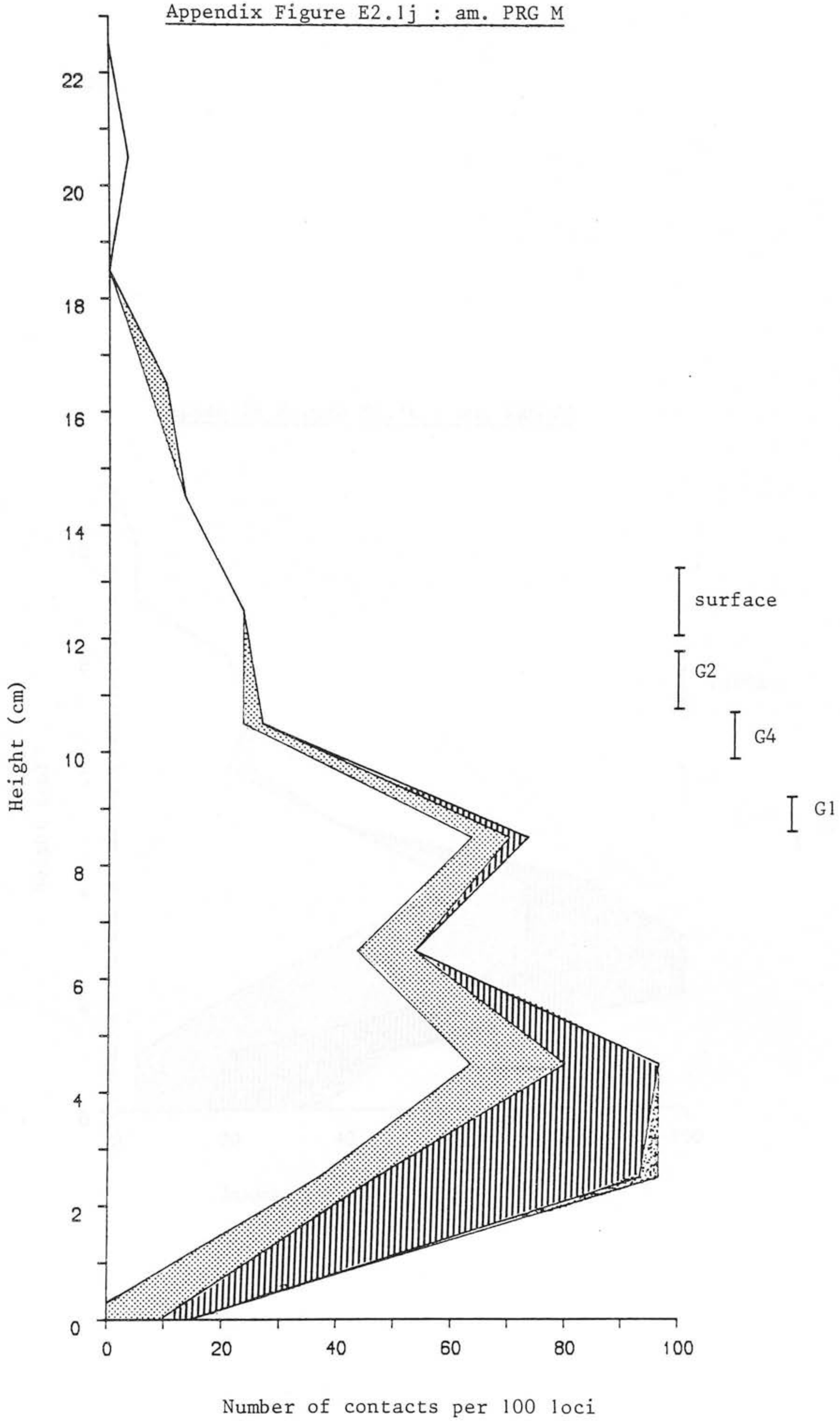
Appendix Figure E2.1h : oats HC



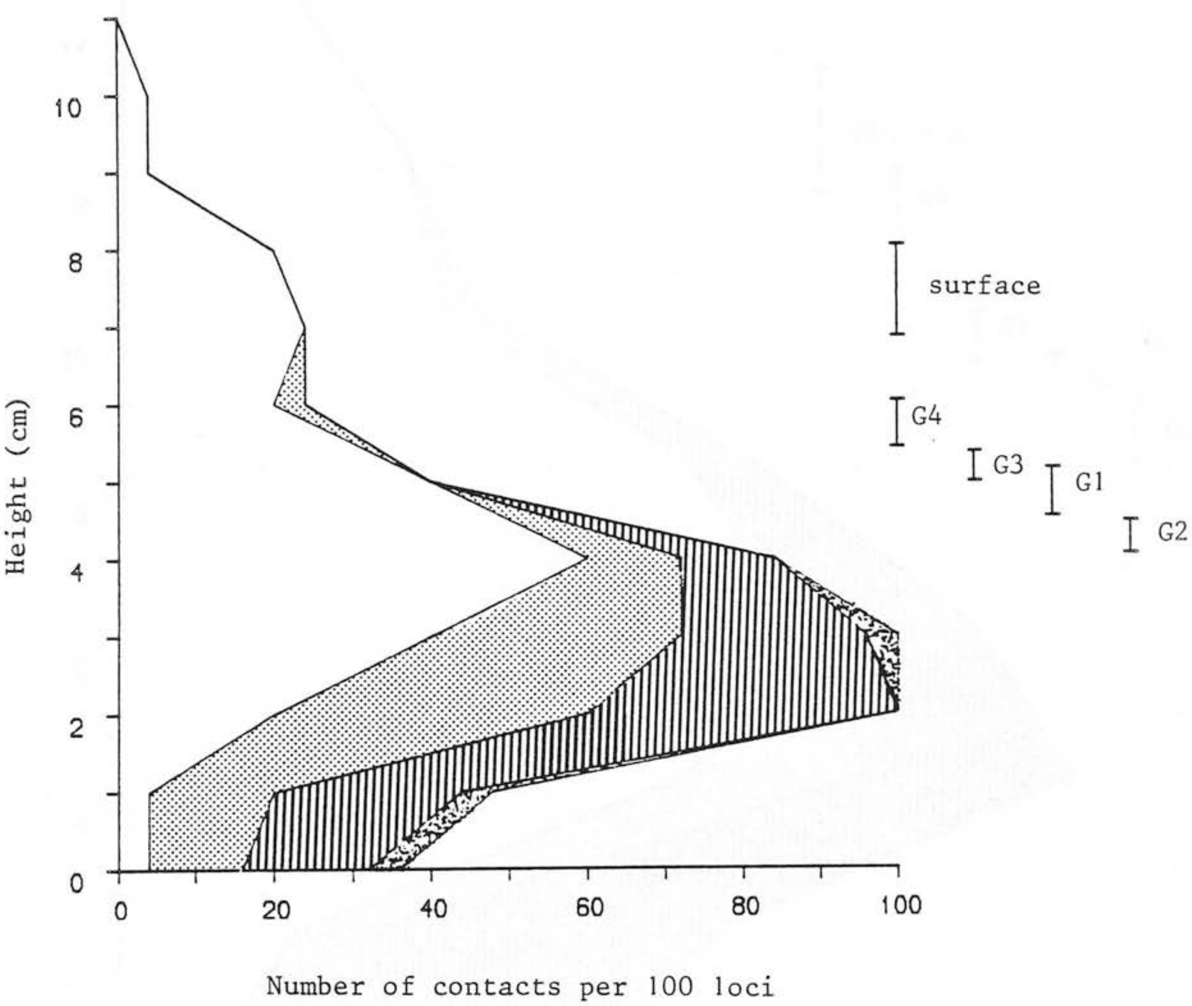
Appendix Figure E2.1i : am. PRG H



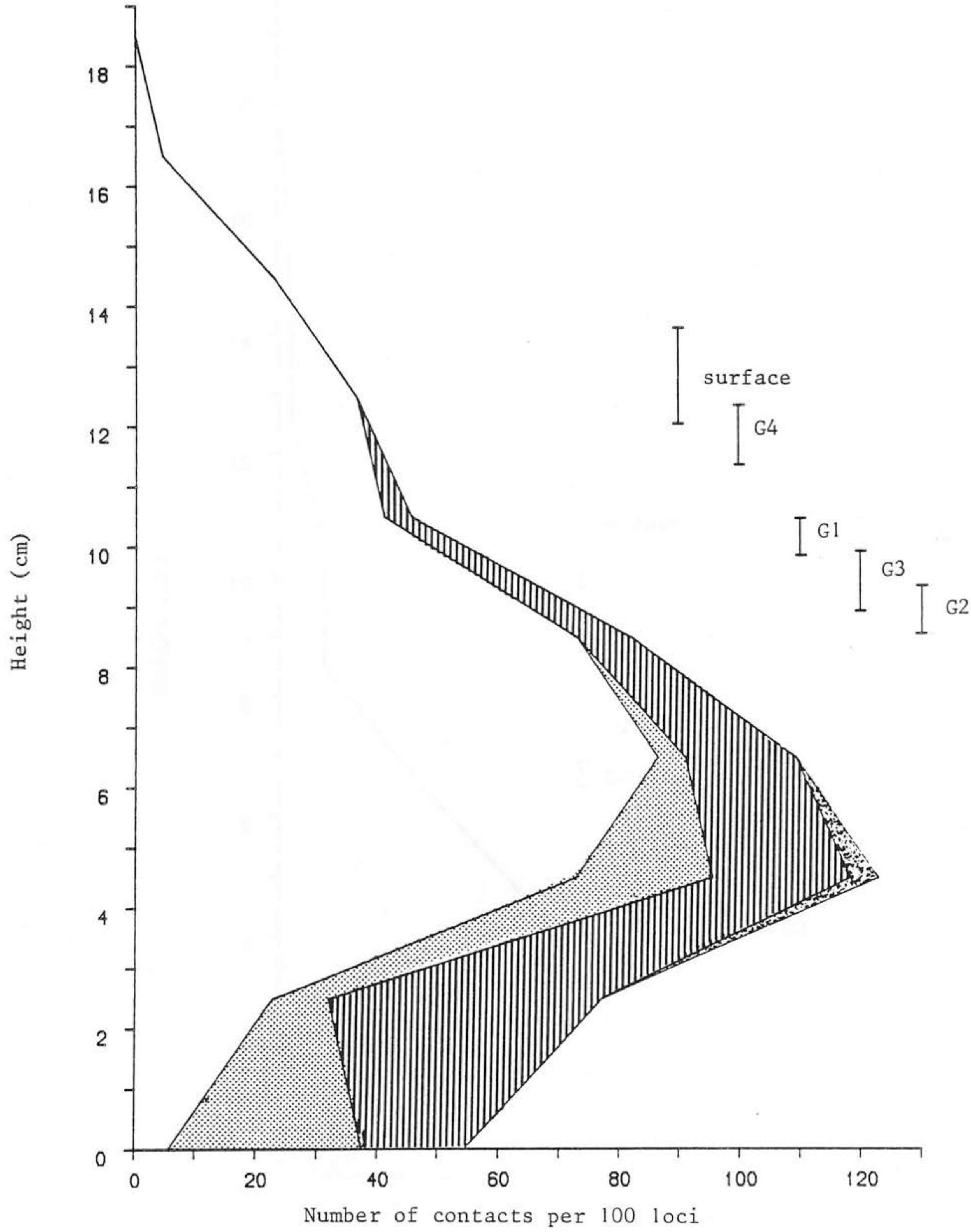
Appendix Figure E2.1j : am. PRG M



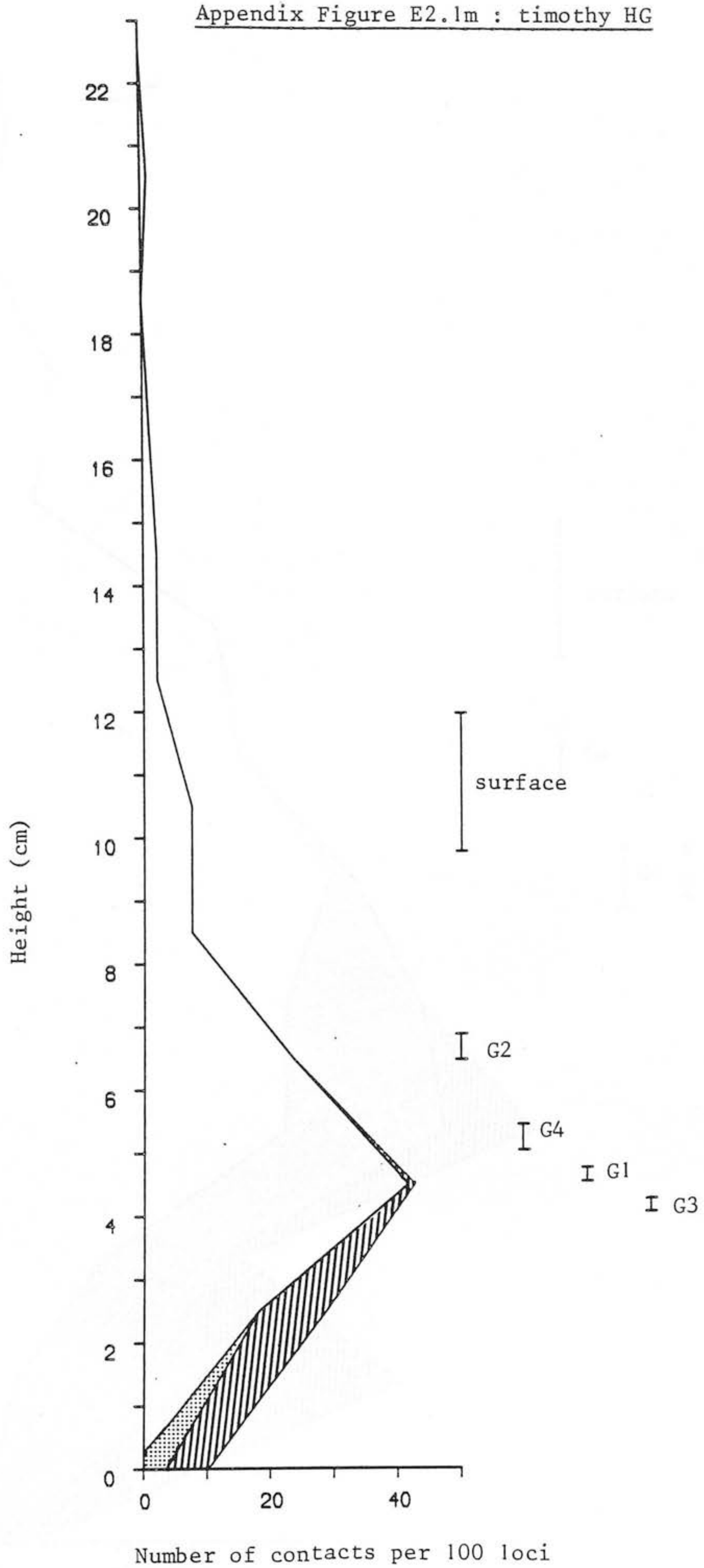
Appendix Figure E2.1k : am. PRG HC



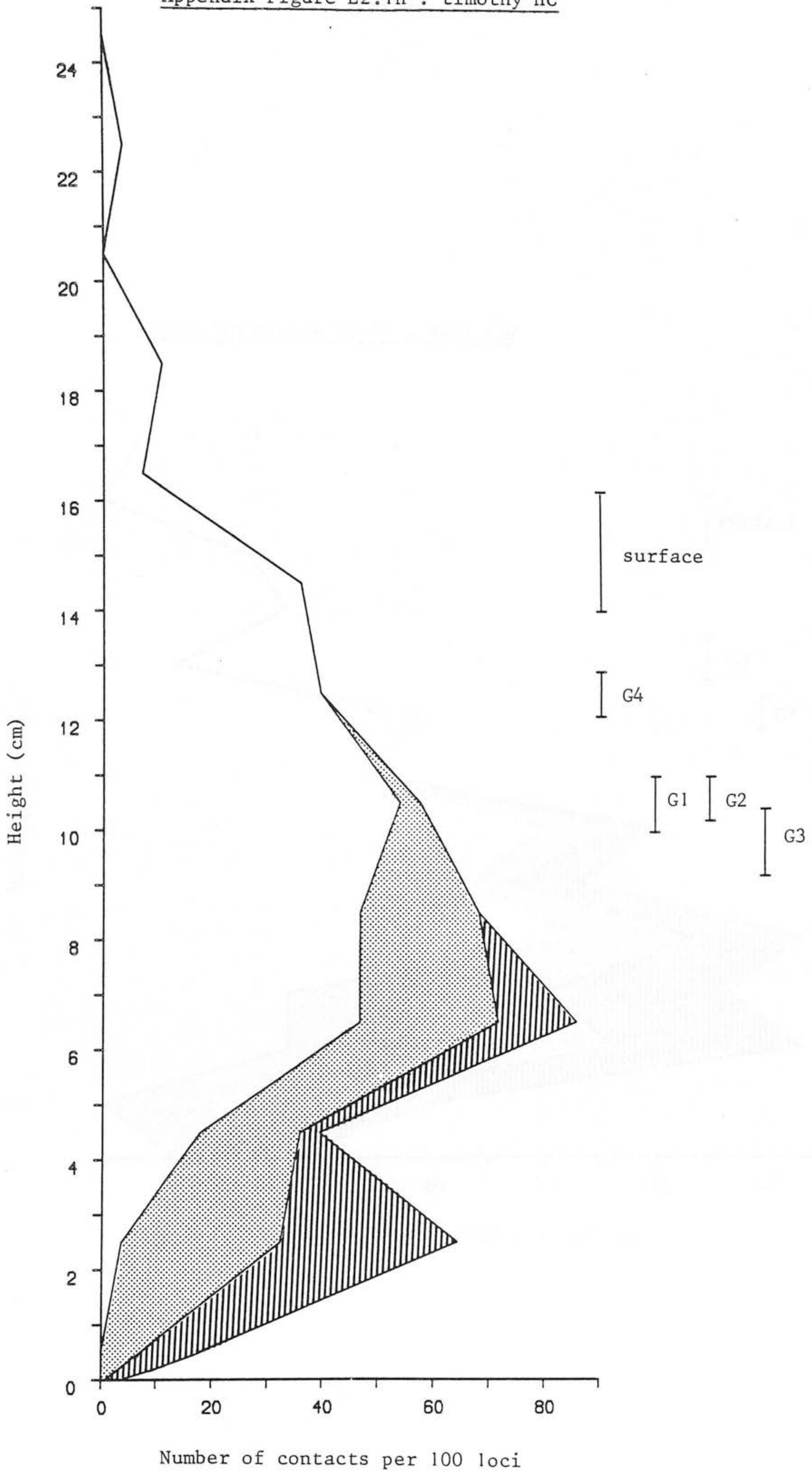
Appendix Figure E2.11 : Agrostis L



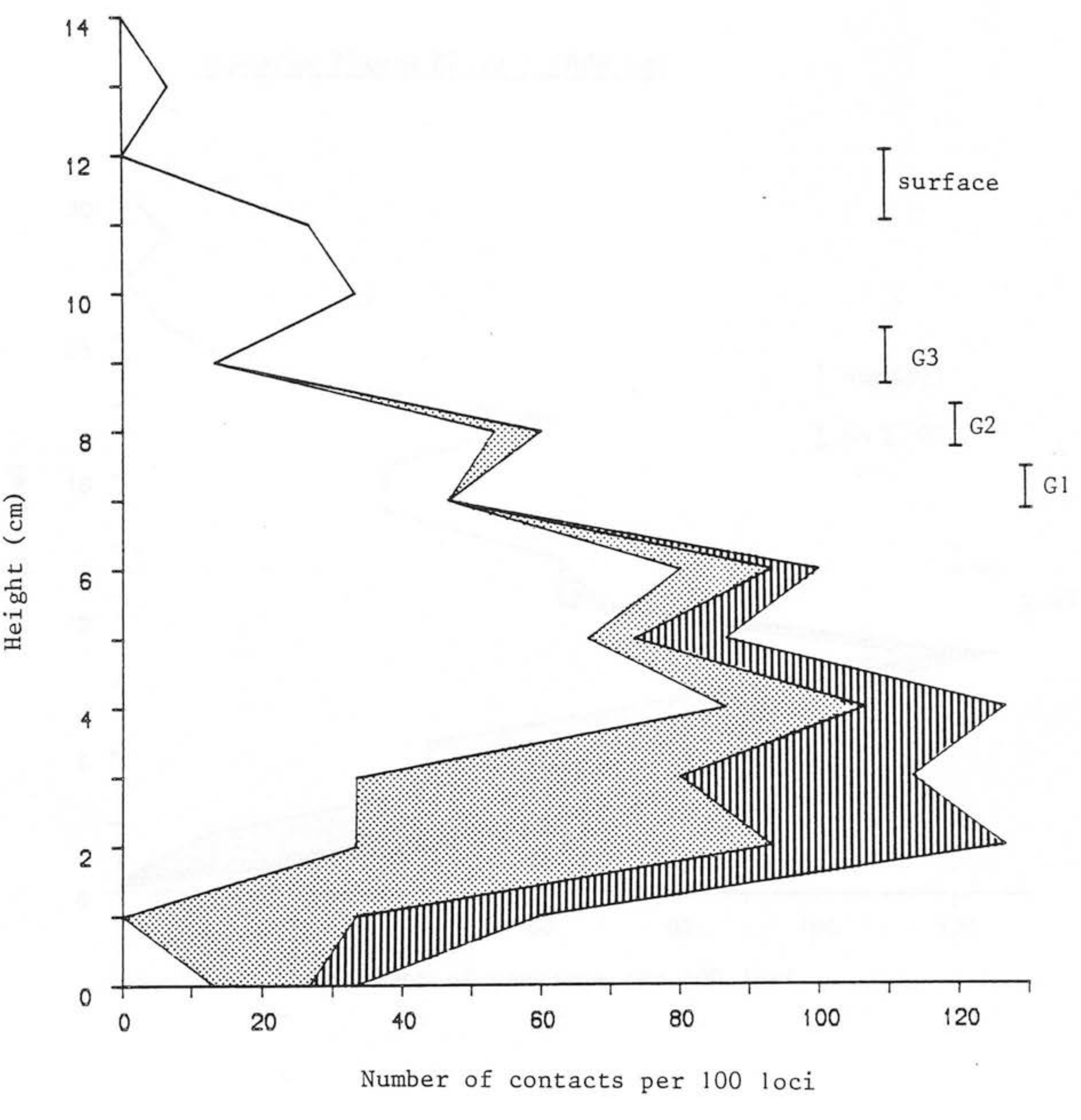
Appendix Figure E2.1m : timothy HG



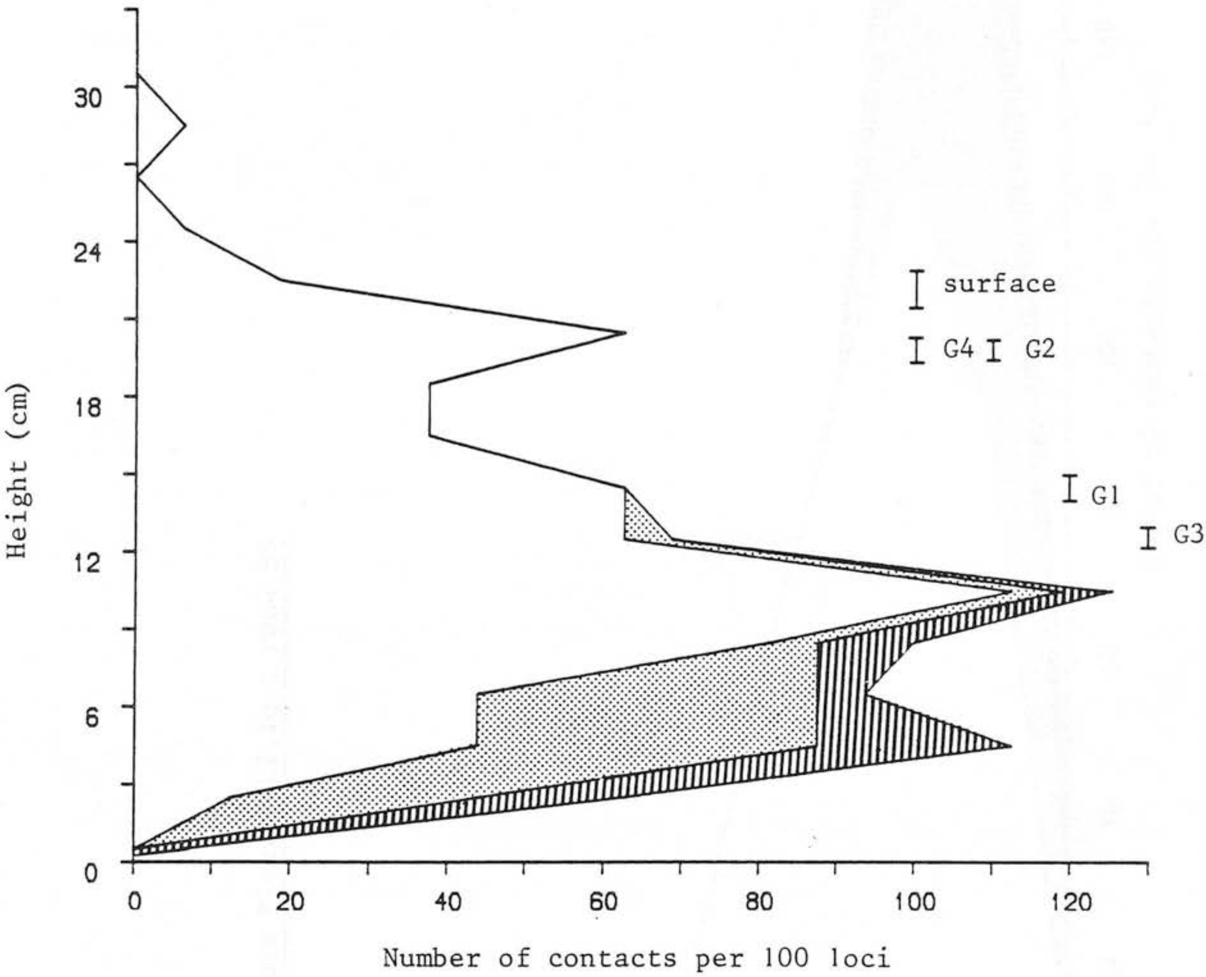
Appendix Figure E2.1n : timothy HC



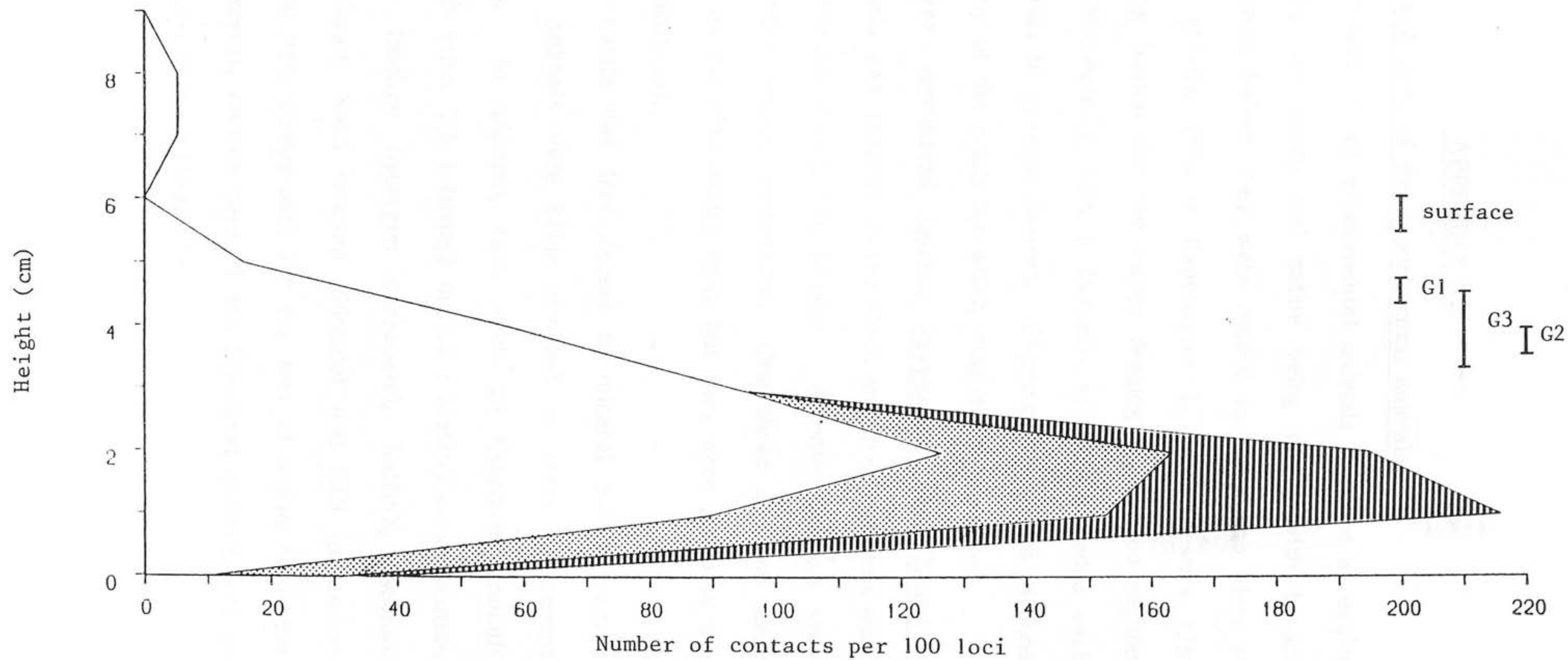
Appendix Figure E2.1o : PRG4 LgP



Appendix Figure E2.1p : PRG4 LgG



Appendix Figure E2.1q : PRG4 SG



APPENDIX 3

Health care of the experimental animals

Routine health care of all experimental animals included a regular worming programme, the sheep and cattle being dosed with broad-spectrum anthelminthics before they were moved to the clean plots at the start of each grazing trial in Experiment 1. Sheep were also wormed before being housed for the indoor feeding trials, and regular foot-trimming and foot-bathing with a formalin solution preceded each grazing or indoor trial to prevent footrot. Clipping took place in June each year, before any of the trials for which results are presented.

All sheep were vaccinated against Pasteurella and Clostridia infection as pneumonia was endemic in the flock and the symptoms were evident in certain animals during hot weather. Affected animals were treated with antibiotics, usually terramycin. One sheep and one steer suffered from bloat on the 1983 barley crop, but they were cured by the administration of arachis oil.

All sheep and cattle had free access to mineral blocks, except when the fistulated animals were being sampled, in order to prevent mineral deficiencies. In addition, each week all fistulated animals received, by stomach tube, 0.5 l (sheep) or 2.5 l (cattle) of a solution containing $NaHCO_3$ (sodium hydrogen carbonate), $NaHPO_4$ (sodium hydrogen orthophosphate), NaCl (sodium chloride) and KCl (potassium chloride), in order to help compensate for the loss of saliva from the fistula. In other respects, routine care of the fistulated animals was as described by Le Du and Penning (1982).

APPENDIX 4

An assessment of the recovery of chromium from sheep dosed twice daily with chromic oxide

Since faecal output in the Experiment 1 grazing trials was estimated from the chromic oxide (Cr_2O_3) dilution technique, a check was made on the recovery of chromium (Cr) under the controlled conditions of an indoor feeding trial. The assessment was made in November 1984, during indoor trial 2 in which the four sheep fed on am. PRG and the four fed on timothy were subjected to Cr_2O_3 dosing and faecal sampling.

In line with grazing trial procedure, each sheep was dosed twice daily, at 09.00 and 15.15h, with a 1-2g paper pellet containing Cr_2O_3. Dosing continued for thirteen days; a five-day run-in period followed by an eight-day measurement period during which faeces grab samples were collected at the time of dosing and bulked into four subperiod collections, each comprising four individual samples. For the last three subperiods, collections were also made of the total faeces produced each day.

All faeces samples were weighed fresh then stored at -18°C until processing. Samples taken from the total collections were oven-dried to assess DM content, and the Cr content of the grab samples and of further samples from the total collections was determined after freeze-drying, milling and mixing, by a modification of the technique used by Williams, David and Iismaa (1962) using atomic absorption spectrophotometry. A sample of pellets was ashed at 450°C overnight to establish the weight of Cr per pellet, assuming all the ash comprised Cr_2O_3.

These measurements allowed the calculation of the proportional recovery of Cr from both the grab samples (GS) and the total collections

(TC). The two recovery figures, termed recovery_{GS} and recovery_{TC} respectively, were calculated as follows:

$$\text{Recovery}_{GS} = \frac{\underset{(\text{g g DM}^{-1})}{\text{Cr concentration in GS}} \times \underset{(\text{g DM})}{\text{daily faecal output}}}{\text{daily dose of Cr (g)}}$$

$$\text{Recovery}_{TC} = \frac{\underset{(\text{g g DM}^{-1})}{\text{Cr concentration in TC}} \times \underset{(\text{g DM})}{\text{daily faecal output}}}{\text{daily dose of Cr (g)}}$$

As one sheep was found to have regurgitated two pellets during the last subperiod of the trial, these data were excluded from the analysis. The remaining data (n=23) indicated that the mean proportional recoveries were: for recovery_{GS}, 0.996 (s.e. 0.0187); and for recovery_{TC}, 0.985 (s.e. 0.0189).

It was concluded that recovery of Cr was virtually complete using both the grab sampling technique and the total collections. Therefore, no correction for recovery was required when estimating faecal output from grab samples in the grazing trials. Twice daily grab sampling did not appear to give distorted recoveries due to diurnal fluctuations in the Cr concentration in the faeces, although this has been a problem in previous experiments (Le Du and Penning, 1982).

APPENDIX 5

An assessment of the recovery of ingested herbage from oesophageal fistulated sheep

Between 29 October and 1 November 1984, a series of hand-feeding trials was run to test the recovery of ingested herbage from a total of thirteen oesophageal fistulated sheep which had been used in Experiment 1. Four of these individuals had also been sampled in Experiment 2.

The sheep were housed for three days, at night in groups in large pens with access to hay, water and mineral blocks, and during the day in small individual pens where they were offered a series of small test feeds of freshly cut and chopped PRG. Each feed weighed 50 g fresh, and the DM content of each set of feeds was determined in triplicate from samples of herbage oven-dried at 90°C for at least twelve hours. Before being offered a feed, each fistulated sheep was prepared as for sampling outside, the fistula being thoroughly washed and any ingested food removed. A foam rubber plug was fitted in the oesophagus just below the fistula and a polythene sampling bag tied round the animal's neck. Sheep were fed simultaneously where possible, to encourage them to eat, and after an animal had stopped eating it was encouraged to swallow several times to expel any material still in the upper oesophagus. The complete sample of extruded material, and any herbage which remained in the feed bowl, were then weighed fresh and after oven-drying.

The feeding trials continued until most animals had been sampled satisfactorily on six occasions. Results were discarded if the foam plug was expelled during sampling or the extrusa samples were seen to be contaminated with rumen contents.

The proportional recovery of ingested herbage is often calculated as follows:

$$\text{Recovery} = \frac{\text{extrusa DM (g)}}{\text{herbage DM offered (g) - herbage DM refused (g)}}$$

[Equation (1)]

However, it was clear that when the recoveries from the current trials were expressed in this way they were inflated due to contamination of the extrusa with saliva DM. Consequently, a correction was made for saliva contamination by calculating the fresh weight, and hence dry weight, of that fraction of each extrusa sample which comprised only herbage, not saliva. The method was reliant upon a knowledge of the following four variables: the fresh weight of the complete extrusa sample; and the DM content of the complete extrusa sample, its herbage and saliva components. The first two variables were measured during the trials, the DM content of the herbage in the extrusa was assumed to equal that of the herbage offered, and the DM content of saliva was found to be 0.0116 (s.e. 0.00034) from oven-drying a single saliva sample collected from each of three fistulated sheep. Equation (2), which was used to calculate the fresh weight of the herbage fraction of the extrusa, was derived as follows:

Let E_D = extrusa DM

H_D = herbage DM in extrusa

S_D = saliva DM in extrusa

E_F = extrusa fresh weight

H_F = fresh weight of herbage in extrusa

S_F = fresh weight of saliva in extrusa

E_{DMC} = DM content of complete extrusa sample

H_{DMC} = DM content of herbage in extrusa (assumed to equal DM content of herbage offered)

S_{DMC} = DM content of saliva in extrusa (0.0116)

By definition, $H_D + S_D = E_D$

Therefore $(H_F \times H_{DMC}) + (S_F \times S_{DMC}) = (E_F \times E_{DMC})$

Substituting E_F-H_F for S_F:

$$(H_F \times H_{DMC}) + (E_F - H_F)S_{DMC} = (E_F \times E_{DMC})$$

$$(H_F \times H_{DMC}) - (H_F \times S_{DMC}) = (E_F \times E_{DMC}) - (E_F \times S_{DMC})$$

$$H_F \quad (H_{DMC} - S_{DMC}) = E_F \ (E_{DMC} - S_{DMC})$$

$$H_F = \frac{E_F \ (E_{DMC} - S_{DMC})}{H_{DMC} - S_{DMC}}$$

[Equation (2)]

The calculated H_F value was then multiplied by H_{DMC} to estimate the herbage DM in the extrusa (H_D). H_D was used in the calculation of the proportional recovery of ingested herbage, corrected for saliva contamination, as follows:

$$\text{Recovery} = \frac{\text{herbage DM in extrusa } (H_D) \text{ (g)}}{\text{herbage DM offered (g) - herbage DM refused (g)}}$$

[Equation (3)]

The results of the recovery trials, expressed as in Equation (3), are given in Appendix Table 5.1 for:

a. the six sheep still available in 1984 from the pool of seven used in Experiment 1 in 1983;

b. six of the seven sheep used in Experiment 1 in 1984 (the other animal refused to sample indoors, and only produced a single sample in the grazing trials);

c. the four animals used in Experiment 2 in 1984; these are individuals 1-4 listed under a.

The results indicated that both within and between individual animals the recoveries were quite variable (mean values ranging from 0.60 to 1.12 and the standard errors from 0.012 to 0.132), but the animals with the lowest mean recoveries (numbers 7 and 12) were not used in Experiment 2 in which the critical estimates of bite weight were obtained directly from the fistulates. The overall mean recoveries were high (0.98, 0.89 and 0.96 for groups a, b and c respectively), and were in line with values obtained in previous work (which were not corrected for saliva contamination). Stobbs (1973a) obtained a mean OM recovery of 0.95 (individual samples ranging from 0.85 to 1.08) from cattle fitted with throatplugs. Jamieson (1975) and Jamieson and Hodgson (1979a) estimated the DM recoveries from calves fitted with throatplugs to be 0.97 (s.e. 0.025) and 0.98 (s.e. 0.014) in two experiments (a calf with poor recoveries was excluded from the latter experiment). Rodriguez Capriles (1973) found the DM recoveries of sheep and cattle sampled without throatplugs to be 0.98 (s.e. 0.105) and 0.98 (s.e. 0.108) respectively.

Each of these authors obtained some recovery estimates which exceeded 1.00, and the same phenomenon occurred in the current work even after correcting for saliva contamination. It was considered that the overestimates were due to the animals retaining small amounts of herbage from previous feeds in the mouth or upper oesophagus.

Appendix Table 5.1

The proportional recovery of ingested herbage, corrected for saliva contamination, from the oesophageal fistulated sheep used in Experiments 1 and 2

Experiment and year		Sheep	Recovery mean	s.e.	n
1	1983	1	1.00	0.017	6
		2	0.85	0.099	6
		3	0.96	0.042	6
		4	1.12	0.047	4
		5	1.02	0.022	6
		6	0.99	0.039	6
		mean	0.98	0.023	34
1	1984	7	0.79	0.132	6
		8	0.98	0.013	6
		9	1.00	0.031	5
		10	0.99	0.015	6
		11	1.01	0.012	6
		12	0.60	0.092	6
		mean	0.89	0.037	35
2	1984	1-4	0.96	0.034	22

APPENDIX 6

The rules applied when smoothing and interpolating between the height/density profiles of a sward measured by stratified clip before, after, and in 1984 during, grazing

The following rules were observed in the treatment of the sward profile diagrams produced from the statified clip data.

1. The maximum density at any particular height was never allowed to exceed the corresponding density of the profile measured before grazing (B). Thus, if as occasionally happened the profile measured after grazing (A) or during grazing (D) had a greater density in the basal strata than the B profile (as in Figure E1.3, Type I swards), the extra density was ignored and the set of profiles drawn with the B line as the maximum density.

The application of this rule meant that the densities of the lower strata of a sward were allowed to decrease with time (as in Figure E1.3, Type II swards) or to remain constant, but not to increase. The increases measured on certain swards would have resulted from herbage being trampled down from higher strata, with these gains in material exceeding any losses due to grazing and uprooting. However, since the measurements taken did not allow the isolation of the independent effects of grazing, uprooting and trampling on sward structure, the complication of a herbage build-up in the lower strata was best avoided. The interest in this experiment centred on herbage removal from the sward, and therefore on the upper part of the sward profile where there was a net loss in material with time, rather than on the lower part where there was a net gain.

2. Aberrant height or density values for the 1984 swards were corrected as follows:

a. On three swards where the measured A profile did not intersect the B profile but had a density at a height of 3 cm of over 0.85 of the B profile density, the A profile was drawn as having the same density as the B profile at and below a height of 3 cm. Due to plot variability, sampling error, and the different strata depths used on subsequent measurement days, the stratified clips were not considered to be sufficiently accurate to be sure that the A profile basal stratum density was substantially less than that of the B profile. In addition, the point quadrat profiles for these plots indicated a similar density in the basal stratum before and after grazing.

b. Corrections were made to the maximum height of certain profiles on nine plots where the original data indicated that the maximum height did not decline as the sward was grazed down. This was undoubtedly due to sampling error, with either tall clumps of weed or a disproportionate amount of ungrazed relative to grazed herbage being included in the stratified clips, and the swards where this occurred were easily identified.

The maximum heights of five B profiles and nine A profiles were considered to have been overestimated in this manner. In order to find a suitable correction factor, regressions were calculated relating the maximum stratified clip height of the satisfactory profiles to the corresponding measurements of a) the maximum profile height measured by point quadrats ($r^2 = 0.81$ $P<0.001$, $n = 26$); and b) the fourth highest (90th percentile) surface height measurement ($r^2 = 0.77$, $P<0.001$, $n = 54$), for the days on which this information was available. Choice of the 90th percentile was empirical; these data were considered to be more robust than the maxima.

The maximum stratified clip height for each of the unsatisfactory B and A profiles was corrected by taking the mean of the values predicted by each regression equation, thereby reducing the risk of bias from using either regression alone. After correcting the maximum heights, straight lines were drawn from these points on the y-axis back to the original profiles, joining at the highest mid-stratum points which ensured that the shape of the modified profiles conformed with the general profile pattern.

Since point quadrat measurements were not taken during grazing, unsatisfactory D profiles could not be corrected in the same way as the B and A profiles. For six of these D profiles, the maximum height, and where necessary also the highest few points of the profile, were found by linear interpolation between the B and A profiles. The measured D profiles for a further three swards were totally discarded because, in contrast to other plots, they did not lie consistently between the B and A profiles. The B and A profiles were considered to be more reliable than the D profiles as they were based on clips taken from a greater number of turves, and they showed a similar pattern to profiles determined by point quadrats.

c. A total of seven aberrant points in various 1984 swards were smoothed by eye to conform with the general profile pattern for those swards.

3. Sward profiles on the required days during the measurement period were derived from the B, D (if measured) and A profiles using the following rules:

a. For the top of the B, D and A profiles, when the density mid-stratum in the highest stratum was less than 0.01 mg DM cm^{-3}, then this was reduced to become the y-intercept. For greater densities in the highest stratum, the y-intercept was taken to be either the upper limit of this stratum or the point of intersection of the profile and the y-axis when the profile was continued in a straight line from its two highest points. The option giving the lower intercept was selected.

b. For the major part of each derived profile, linear interpolation in a vertical plane (i.e. at a constant density) was applied between the B and D, D and A, or B and A profiles, as appropriate.

c. The lower sections of the B, D and A profiles were extended down in a straight line to intersect the B line, D line or ground level as appropriate. Points on the derived profiles continued to be determined by linear interpolation down the profile until a predetermined mid-stratum point on the upper measured profile was reached (point P). If the two measured lines converged below point P, then the derived profiles were extended down parallel to the lower measured line until reaching either the B line, D line or ground level. If, on the other hand, the two measured lines diverged below point P, then the derived profiles were extended in a straight line from the last two interpolated points until they reached either the B line or ground level.

A degree of subjectivity was involved in defining the rules which determined the derived profiles, and decisions about the lower sections of the profiles were probably of greatest consequence to the subsequent calculation of the median grazed stratum bulk density. Therefore, the swards were treated as consistently as possible, and for example point P was the second highest mid-stratum point on the upper measured profile, except in a few cases where this would mean that the general pattern of profiles was not maintained and a more suitable mid-stratum point was selected. The two or three swards per crop were always treated similarly, with point P at a constant height, when their measured sward canopy structures were similar.

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